Trilobita: phylogeny and evolutionary patterns

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TRILOBITA: PHYLOGENY AND EVOLUTIONARY PATTERNS

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ABSTRACT

TRILOBITES have been cited in the scientific literature for nearly 200 years but their evolutionary relationships are contentious. Studies resolving this issue are necessary in order to assemble a stable trilobite classification and also to facilitate further macroevolutionary studies on the group. However, less than fifty papers have been published using modern cladistic methods.

This work investigated the phylogenies of four large trilobite groups: Lichoidea, Calymenina, Odontopleurinae and Illaenoidea. These four taxa have distinctive gross morphologies and present different challenges. Some taxa are well-known, others poorly; some are spiny and some exceptionally effaced. Fine resolution was attained in all resulting phylogenies. The systematic palaeontology of each group was reassessed accordingly and phylogenetically valuable character states were listed.

A Bayesian phylogenetic method was employed in Chapter 2 to analyse morphological data for the first time: lichoids were used as a case study. The trees obtained were similar to those inferred using parsimony, with the exception of relationships between the deeper branches.

Chapters 4 and 5 investigated the phylogeny of two large groups (odontopleurids and illaenoids respectively) and used the same character data to explore the *disparity* (morphological variety) of both groups. The disparity of odontopleurids decreased significantly through time, but that of illaenoids did not. The relative disparity of major clades within each group was also investigated.

In summary, the results of this study provide a platform for future trilobite workers: important morphological distinctions have been identified between clades, phylogenetically-important character states recognised and temporal patterns of disparity for two higher taxa have been investigated.

ACKNOWLEDGEMENTS

FIRST, many thanks to my supervisors, Matthew Wills and Richard Fortey, whose writings inspired me for many years before we even met. (What a wonderful opportunity you gave me: to be able to study my very favourite thing for so long!) Thanks to Matthew for everything: especially his help with all things numerical. I am very grateful to Richard for trilobite (and fungi) inspiration and lots of thought-provoking, happy Oxford afternoons.

I am enormously indebted to Euan and Cecilia for agreeing to supervise me all those years ago in Edinburgh – for opening my eyes to the wonderful world of fossils – and for their continued support and valued friendship.

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To 10 Belgrave Crescent: for being a stimulating haven to write-up in. Helen Haste kindly provided a comfortable and happy atmosphere. And to the late Bev Halstead, who provided me with a wonderful, well-cherished library and, if he still disagrees with my cladistic methods, let it be...

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I thank my parents especially for all their personal sacrifices in order that I can make life-choices selfishly and without restriction. This work is dedicated, in its entirety, to them. Thank you so much.

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1. Introduction

1.1 WHAT ARE TRILOBITES: WHY ARE THEY USEFUL SUBJECTS?

'...[the] butterflies of the sea...' – Levi-Setti 1995, p. 1

VERITABLE zoological time-capsules lie beneath our feet in the form of fossils. One such fossil group, the trilobites, were marine arthropods that teemed aplenty in Palaeozoic seas. As such, these extinct animals have provided us with a detailed insight into life half a billion years that passed before we came to be; with a history extending through some three hundred million years.

The first published mention of trilobites in scientific literature concerns a specimen of what is now known as *Ogygiocarella (Asaphus) debuchii* Brongniart, 1822 (see Figure 1.1).

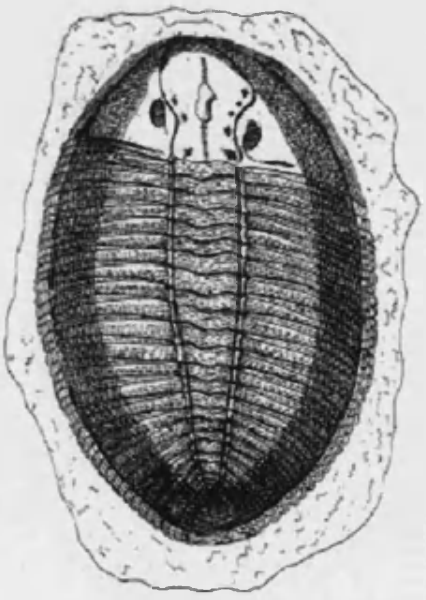


Figure 1.1: The *Sceleton of some Flat-Fish* described by Dr. Lhwyd (1698).

As is the case with all rigorous fields, our body of knowledge is in a continual state of flux as hypotheses are reassessed and readdressed. Scientific concepts regarding trilobites have duly developed since their first description. They were recognized as a formal animal group in 1771, by Walch, and then re- evaluated by Ramsköld and Edgecombe (1991) and, later, by Edgecombe and Ramsköld (1999).

There are many reasons why trilobites have been, and continue to be, interesting and useful subjects for study. They are: (1) among the earliest known arthropods found in the fossil record (Fortey & Owens 1997 *in* Kaesler 1997); (2) they were capable of rapid evolutionary change (Fortey & Chatterton 1988); (3) they showed highly disparate morphology within the class and some unusual and striking appearances; (4) they are found world-wide; (5) they are abundant and (6) can be exceptionally well-preserved.

Trilobites have been the subjects of a vast range of studies, ranging from those concerned with: microevolution (Sheldon 1987), macroevolution (Wills *et al.* 1994), heterochronic changes (McNamara 1978, 1981), to biogeography (Cocks & Fortey 1988). The first phylogenetic study involving trilobites, however, was only published in 1977 (Eldredge) and publications of trilobite cladistic analyses have only featured fairly abundantly over the past decade or less (see references within section 1.3.2).

This work investigates, and makes important steps towards resolving, the phylogenies of four major, contrasting groups of trilobites. It is hoped that the overall work will provide new morphological characters for future workers on similar groups and provide further resolution of general trilobite phylogeny.

The explanations for choosing the groups examined here are documented below:

1 Lichids – This is a well-documented group, with much ground work done and clear morphological groups. Work on this group highlighted many of the common problems inherent in applying morphological phylogenetics to most arthropod groups.

2 Calymenids –The relationships between them and the homalonotids has long been discussed. Dr. D. J. Siveter's expertise, comprehensive library and collection were invaluable.

3 Odontopleurids – This is an exciting and challenging group. Very detailed work on some groups has been conducted by Ramsköld but there remain many gaps. His work helped to develop a framework for this study. Being a very spinous group, it was thought an appropriate clade in which to investigate temporal patterns of disparity.

4 Illaenids and styginids – This group is poorly understood with little documentation on their phylogeny. This proved to be the most challenging group to work on – but it was hoped that it would prove valuable for workers of all effaced trilobites. This group is so effaced that it was thought interesting to test their disparity – to see if they displayed a different pattern compared with the spinous groups.

1.1.1 General Morphology

Trilobites have long been known for their expression of exquisite shapes and sizes (see Plate 1 (a-g)). Indeed, in recent years, a lucrative trilobite-trade has emerged – with trilobite collectors paying extremely large figures for some of the most exceptionally preserved and unusual morphologies. Trilobites have become a kind of geological Van Gogh: their 'art' appreciated long after their prime.

Naturally, the scientific community is interested in more than just the intrinsic beauty of these arthropods. And, indeed, much progress has been made in recent years in the details of trilobite morphology. This has created a rich field for functional morphological studies. Most investigators have been forced to focus on the calcified parts of the trilobite alone as the ventral and internal structures are not often preserved in enough detail. Calcification stops at the inner edge of the doublure, as it rolls ventrally, and, as the limbs are not calcified, often only the dorsal exoskeleton is preserved. In rare circumstances, however, conditions have been appropriate for good preservation of non-calcified structures (at sites known as *Konservat-Lagerstätten*, such as the Burgess Shale of British Colombia, Canada). These sites of exquisite preservational status allow us windows into the structure of soft-bodied animals (Plate 2 (a-b)), microscopic embryonic stages of early Metazoa (Plate 2 (c-d)), the delicate internal structures of fossil organisms (Plate 3 (f-h)) and even behavioural characteristics (Plate 2 (e-f)).

A short description of the trilobite body follows (see Kaesler 1997, for a fuller explanation). The terminology of the *Treatise on Invertebrate Paleontology* (Kaesler 1997) is followed throughout this thesis unless otherwise stated (see Figure 1.2).

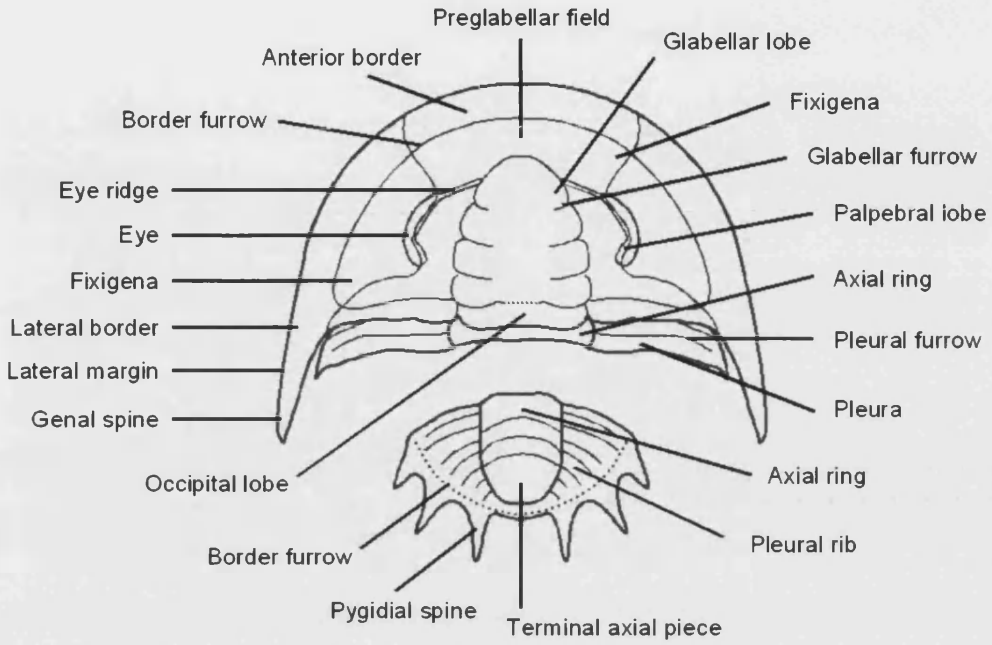


Figure 1.2: Terminology of the dorsal exoskeleton (adapted from Clarkson 1998).

Plate 1.
Various morphologies expressed by the class Trilobita: (a-b) the phacopoid, *Erbenochile* sp., with unusually high eyes (Fortey & Chatterton 2003, figs 1b and a, respectively; x 1.0); (c) spiny *Lichas (Hoplolichas) tricuspidatus* (www.paleoart.com); x 1.0; (d) *Cybele* sp. (www.paleoart.com); x 1.0; (e) a highly effaced asaphid (www.paleoart.com); x 1.0; (f) a trinucleid displaying the possibly sensory pitted fringe (http://www.lapworth.bham.ac.uk/collections/palaeontology/lowerpalaeozoic.htm); x 0.5; (g) the highly tuberculate cranidium of *Phacops rana* (http://www.phacops.com); x 0.5.

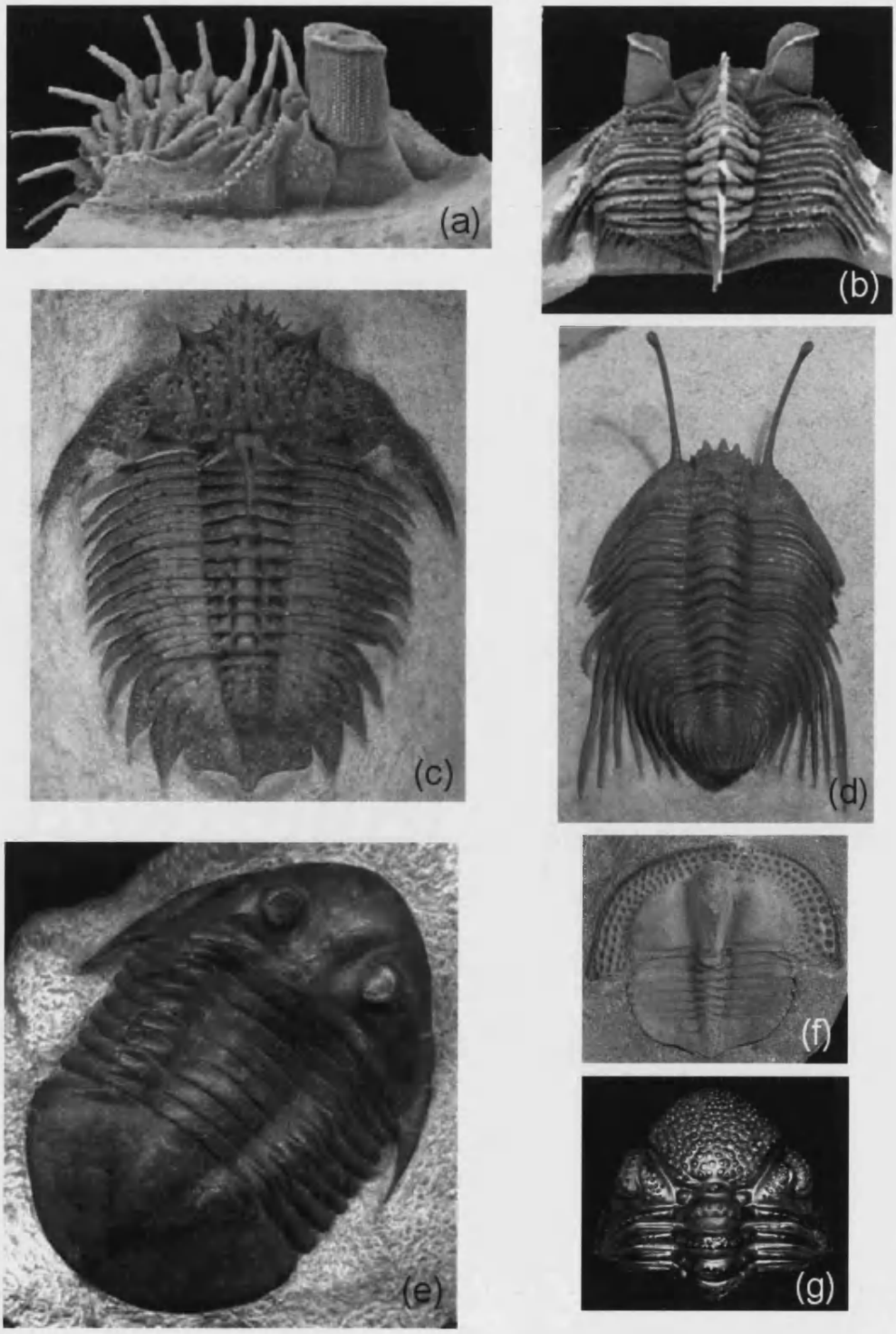
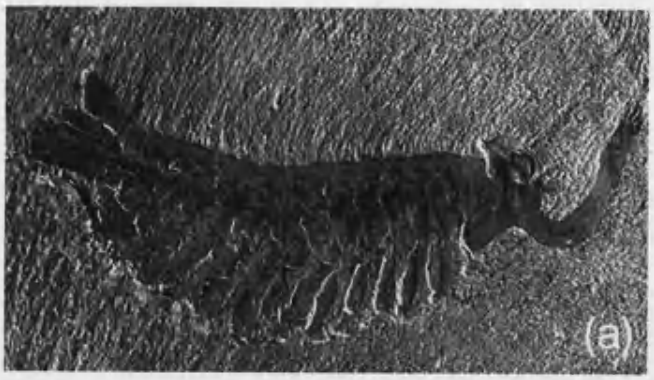
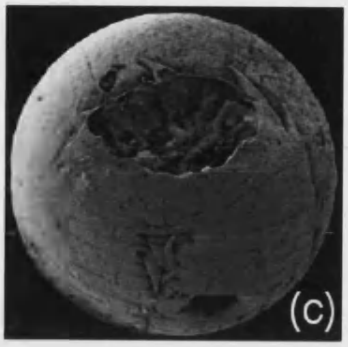


Plate 1





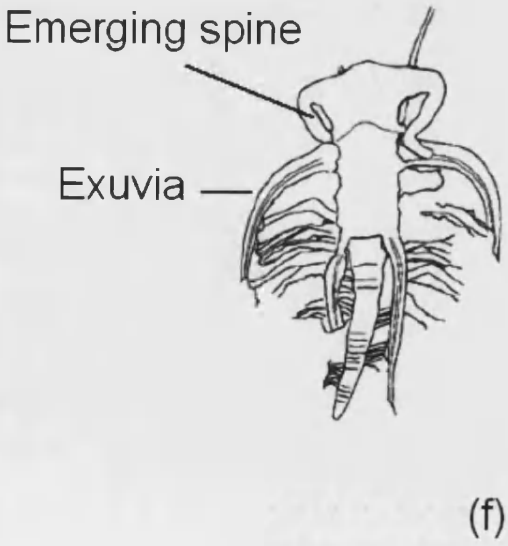


Plate 2

Plate 2.
(a-b) *Opabinia regalis* (from Briggs *et al.* 1994). (a) fossil; (b) reconstruction; x 0.5.
(c-d) Late-stage embryos of *Markuelia hunanensis* from the middle and late Cambrian Bitiao Formation of Wangcun, Hunan Province, south China (from Dong *et al.* 2005). (c) Embryos of *M. secunda* from the early Cambrian Pestrotsvet Formation at Dvortsy, Siberia. Fracture reveals serially-repeated internal organs in register with surface annuli; x 400.0; (d) anterior pole of embryo exhibiting multiple circumoral rows of spines; x 100.0.
(e-f) The oldest known fossil of an arthropod in the act of moulting: *Marrella splendens*, from the Middle Cambrian Burgess Shale of British Columbia, Canada. (e) Specimen of *M. splendens* emerging and pulling out the flexible lateral spines from the old exoskeleton (exuvia; scale bar 5 mm); (f) *Camera lucida* drawing of the same specimen (both from García-Bellido & Collins 2004).

Dorsal. The dorsal, exoskeletal cuticle of trilobites was calcified (as was the hypostome and doublure), composed of low magnesian calcite of considerable purity (Wilmot & Fallick 1989) and 100-150μm thick on average (Fortey & Wilmot 1991). Its primary function may have been to provide musculature support: invaginations occurred in the form of glabellar furrows, to which the musculature operating the cephalic appendages attached. Even those trilobite species that show effaced glabellar furrows display muscle insertion areas as dark patches (e.g. the Homalonotidae of Chapter 3).
This cuticle is often modified into spines: most species display genal spines but some species are extremely spinous all over the exoskeleton (e.g. the Odontopleurinae of Chapter 4). It has been suggested that these have many functions:

- Genal spines providing a 'lever' to aid the moulting process;
- Lateral spines to prohibit yawing in the water column and, hence, aid swimming (Fisher 1975);
- Protection;
- Camouflage; and
- To possibly act as an aid to pelagic habits by inhibiting sinking (Hammann & Rabano 1987).

The cuticle is known to have perforations in the form of canals (Stürmer 1980): although the function cannot be ascertained, it is likely that there were sensory hairs, or similar, innervated from these canals (Fortey & Owens 1999). Some species possessed an organ in the form of pits on the occipital lobe (e.g. *Bronteopsis*, see chapter 5): the function of this is unknown but it may have been chemosensory (Whittington 1956, pl. 2, fig. 21).

Ventral. The appendages of meraspid developmental stages (see section 1.1.2 below) of *Agnostus pisiformis* from the Upper Cambrian of Sweden are the best preserved (Plate 3, part (d); Müller & Waloszek 1987). The cephalon bore four pairs of appendages, five pairs of trunk limbs (similar to the fourth cephalic limb) follow and reduce in size progressively. A reconstruction of *Olenoides serratus* from the Burgess Shale formation shows antennae and 16 pairs of biramous appendages (probably 3 on the cephalon, 1 pair on each of the seven thoracic segments, and 6 on the pygidium; Whittington 1980; see Plate 3, parts (f) and (h)).

The biramous appendages consist of a walking leg (endopod) and a filamentous gill (exopod). Spines on the coxa bases (gnathobases) would have helped to break up food as it was passed up to the plate overlying the mouth (hypostome).

Plate 3.
(a) *Peltura scarabaeoides* protaspis, Rössånga, Sweden; x 25.0; (b) Schizochroal eye of *Phacops latifrons* (Bronn) from the Devonian of Germany (Levi-Setti 1995); x 5.0; (c) *Phacops rana*, Ohio, U.S.A. This shows a newly-moulted soft-bodied trilobite (left) that perhaps died close to the remains of its cast-off exoskeleton (right); x 3.0; (d) Reconstruction of the ventral anatomy of *Agnostus pisiformis* (Wahlenberg) (Müller & Waloszek 1987); x 50.0; (e) *Paralejurus dormitzeri*, Czech Republic. Holochroal eye is coated with NH_4Cl to increase contrast; x 10.0; (f) *Olenoides serratus* (Rominger 1887, p. 51), with appendages from the Middle Cambrian of the Burgess Shale (Whittington 1980, pl. 20, fig. 4); x 5.0; (g) four aspects of an enrolled calymenid (from Fortey 2000); x 2.0; (h) *Chotecops* and the remarkable preservation of its appendages (Bartels, Briggs and Brassel 1998); x 2.0.
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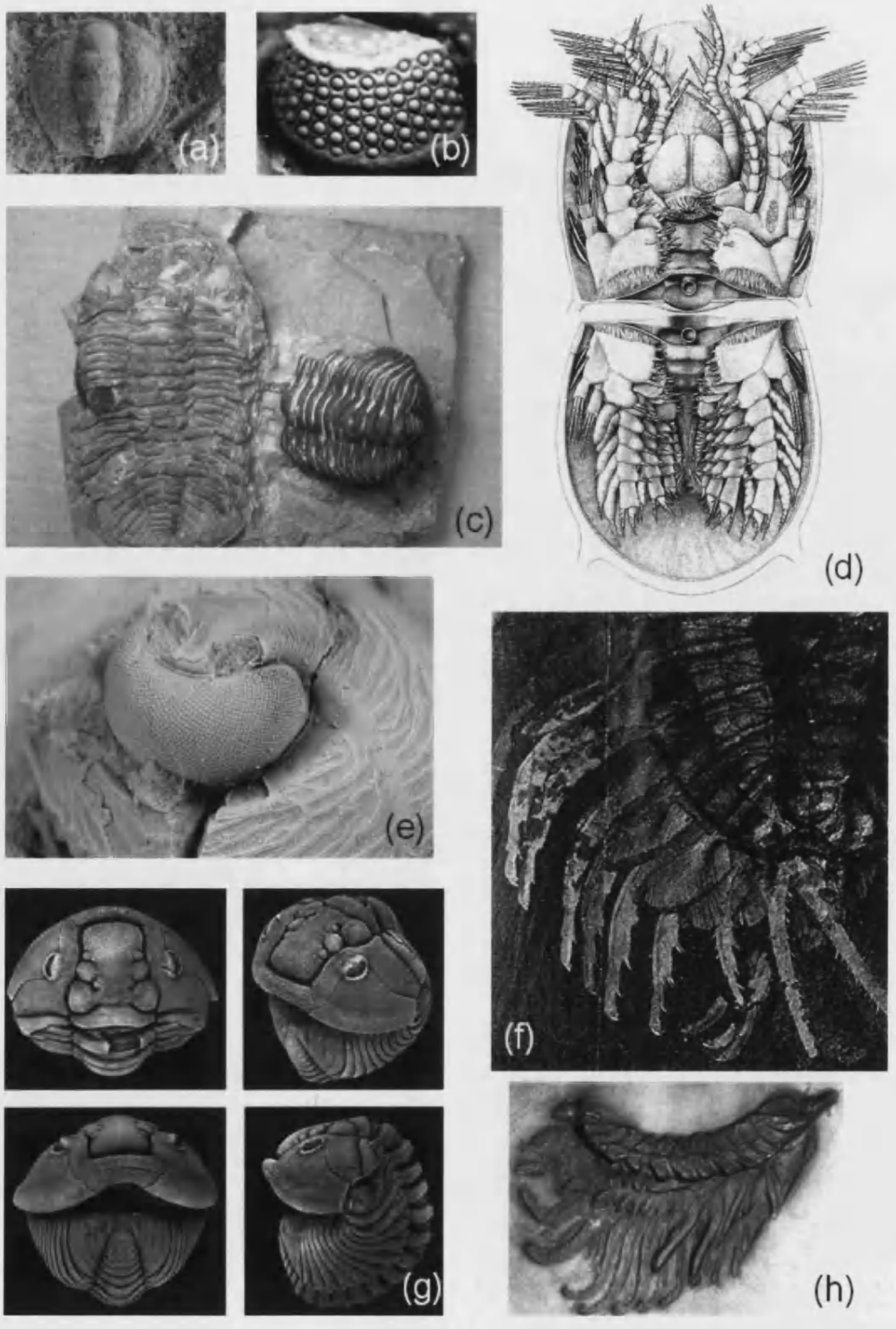

Plate 3

Internal. The forms of muscle scars and of invaginations of the exoskeleton around the axial region have helped elucidate the pattern of limb and ligament musculature (Cisne 1974; see Fig 1.3). Radiographs of pyritized specimens have also been important (see Stürmer & Bergstrøm 1973). Soft parts are unknown so inferences have relied on comparison with biomechanically-similar extant arthropods.

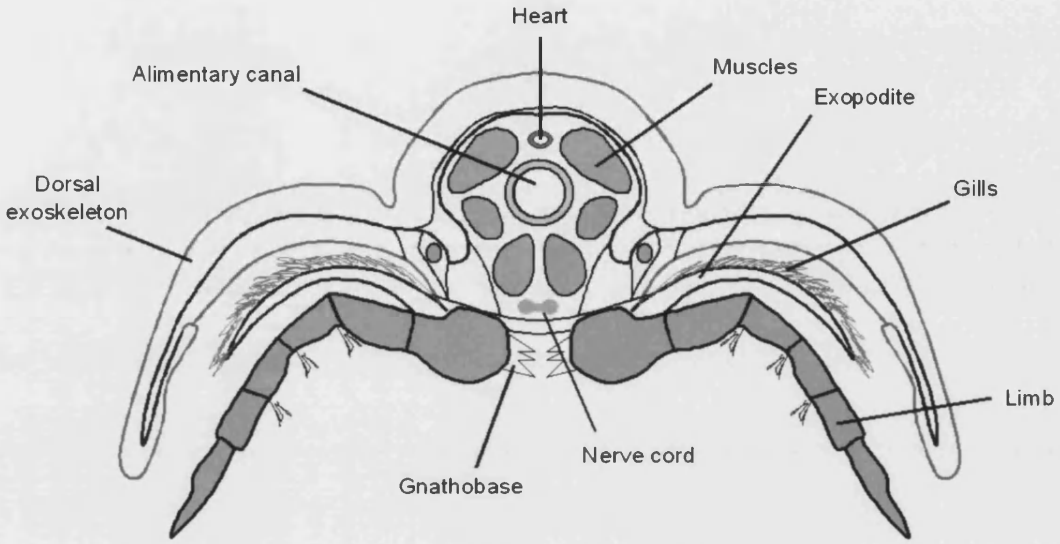

Figure 1.3: Sagittal section of trilobite displaying internal structures.

Behavioural and sensory. Trilobite eyes are the earliest to be preserved in the fossil record (Parker 2003). Eyes are present in the earliest trilobites and their absence is always secondary. The eyes of the later trilobites are better known: the earlier ones possessed a suture (= eye socle) that enabled the visual surface to fall out and are, therefore, rarely preserved in place (Clarkson 1975). They typically comprise an elongate lobe with a large number of lenses. They display two forms: schizochroal and holochroal (Plate 3, parts (b) and (e) respectively). The latter type is simpler and has numerous, hexagonal, small, closely-packed lenses. The former, in contrast, has comparatively few, large lenses that are separated by a sclera. Unusual eye forms are seen in some species, such as *Erbenochile* (Plate 1, parts (a-b)), and blindness is seen throughout the group Trilobita, e.g. *Thomastus* (see Chapter 5) and *Conocoryphe* (see Cotton 2001).

The segmented and articulated trilobite thorax enabled considerable flexion in the dorsoventral plane and, therefore, many trilobites could enrol (Plate 3, part (g)). The commonest form involved the pleural tips of the thorax sliding over each other (in effect shortening the body laterally) while the axial region extends by way of exposing the axial half-rings until the cephalon and the pygidium were brought into close contact.

Trilobites increased their size by moulting. Increase in size occurred during the 'soft' phase: recalcification occurred at the larger size. Individuals would have been most vulnerable at the 'soft' stage, immediately after moulting (see Plate 3, part (c)). Shedding the exoskeleton was a delicate procedure and would have sloughed the limbs, gill branches and antennae as well as the cuticle (Fortey & Owens 1999). Sutures of the exoskeleton would have expedited the process and allowed the trilobite to moult in stages rather than emerging from the exoskeleton in one phase.

Exoskeletal growth in arthropods occurs in a stepwise manner; post-embryonic development being paced by the moult cycle. Some trilobite species adhered to *Dyar's rule* (which assumes a constancy of the postmoult/premoult size ratio between moults), e.g. *Aulacopleura konincki* (see Fusco *et al.* 2004) and *Leptoplastus salteri* (see Pollitt 2001).

1.1.2 Trilobite ontogeny and body patterning

Trilobites calcified their dorsal surfaces relatively early in ontogeny, and their moulting habit yielded sequential instars that can be arranged into ontogenetic series, now known for many species (Chatterton & Speyer 1997). The earliest instar – a single, fused shield - is known as the *protaspis* (Plate 3, part (a)). This was composed of a cephalic region made up of serially-repeated segments (most visible in the axis). Cephalic segments remain stable in number with the appearance of the cephalon changed markedly during growth. The proto-pygidium was characterised by the appearance of additional segments that increased their relative proportions relatively rapidly through growth, but which resembled one another closely in overall form (Hughes 2003). There appear to be two types of protaspid stage – an adult-like and nonadult-like body plan. The latter are more globular and three dimensional in shape, rather than disc-shaped. The transition between nonadult-like and the further adult-like stages of the same species has been interpreted as an example of *metamorphosis* (although this

transition is not the radical reorganization of body patterning to which the term is commonly applied among extant arthropods; Williamson 1982).

The transition to the next major phase – the *meraspis* – was defined by the appearance of an articulation between the cephalon and the trunk region (yielding a hinge-like body structure) and release of segments in a ratchet-like manner. This stage is not developmentally homogenous among all taxa: in many species it occurs after the budding of 3 or 4 thoracic segments, but the cheirurid *Ceraurinella typa* did not seem to reach this stage until it had 14 trunk segments (Whittington & Evitt 1954).

The transfer of segments from the anterior transitory pygidium (a subterminal growth zone) to the thorax continued throughout meraspid ontogeny until the final phase was reached: this is generally considered to have begun at the point at which a stable number of thoracic segments was reached (Raw 1925) and is termed the *holaspis* phase.

1.2 PHYLOGENETICS: A (VERY) BRIEF HISTORY

'The first step to wisdom, as the Chinese say, is getting things by their right names' – *Wilson 1998, p. 2*

The inventory of known living species currently stands at ~1.7 million (Tudge 2000, p. 6) but estimates of numbers of *existing* species are nearer 30 million (see Erwin 1982) or even 100 million (study by Erwin *in* Morell 1999)! The function of science is to uncover things that can help us understand the Universe more fully. A first step toward understanding is to provide a common frame of reference by naming surrounding objects.

Wilson suggested there exists two kinds of original thinkers: those who, upon viewing disorder, try to create order, and those who, upon encountering order, try to protest it by creating disorder: 'The tension between the two is what drives learning forward' (Wilson 1998, p. 46). Indeed, he notes that 'human beings are obsessed with building blocks, forever pulling them apart and putting them back together again' (*ibid*, p. 53). These inclinations may explain our need to look for a natural structure within our fellow creatures and, moreover, why it is constantly unstable.

The history of classification has passed through roughly four phases (see Tudge 2000 for a comprehensive description):

(1) Ancient taxonomy: best represented by Aristotle (384-322 B.C.)
(2) Classical taxonomy: Linnæus proposed his formal rules of grouping and ranking that, with only minor modifications, should endure forever (1758).

(3) Darwinian taxonomy: Darwin (1859) realized that Linnæus' taxonomy and the relationships between species (i.e. a phylogenetic tree) are intrinsically linked. A chronologically equal method to that of cladisitics, but pre-cladistic in current methodological dominance, is *phenetics* or *numerical taxonomy*. It gained much attention from the 1960s onwards but has little following now. The method essentially relied on drawing-up lists of similarities and differences between taxa: the more the merrier. These data were then analysed statistically. Homologous and homoplastic characters were not identified, neither were characters polarized. The subjectivity of the phenetic method has meant that it has been abandoned for the more objective, hierarchical method of cladistics (see Ridley 1986, p. 83-85) that assumes common descent.

(4) Cladistics: Hennig proposed the method *cladistics* (from the Greek *clados*, meaning *branch*) in 1966. It seeks to group taxa according to their shared derived homologies (or synapomorphies). Other features, no matter how conspicuous, are ignored. This method is extremely thorough: vast quantities of morphological data can be collected. This data is analysed by computer in a parsimonious manner (in a way that makes the least assumptions and needs fewer explanations). The nestings produced by this method equate to clades (or groupings) within a phylogenetic tree. These can then be used to instruct the naming of the group in question. Important concepts here are: *monophyletic* (includes the most recent common ancestor plus all descendents), *paraphyletic* (as monophyletic plus only some descendents) and *polyphyletic* groups (does not include the most recent common ancestor).

1.3 THE PHYLOGENY OF TRILOBITES: AS CURRENTLY KNOWN

'...naming is taming' – Fortey 2004, p. 117

1.3.1 The Trilobita sensu stricto

Although trilobites are an abundant and well-studied group, a formal diagnosis of Trilobita has, until recently, remained elusive. Historical diagnoses were little more than general descriptions of a non-specific individual – rather than rigorous appraisals of the distinguishing characters of the group. There have been three main areas of contention:

(1) Whether or not the naraoiids should be considered as trilobites has been disputed. These arthropods lacked a calcified cuticle, evidence of sutures and other important apomorphies of the group Trilobita. The view that they are closely related to the Chengjiang taxon *Retifacies* Hou *et al.* 1989 has been suggested (Hou & Bergstrøm 1997; although this view has been strongly contested, see Edgecombe & Ramsköld 1999). A more favoured view is that they are, indeed, closely related to the Trilobita (Briggs *et al.* 1992; Fortey & Theron 1994; Whittington 1977): they have a large pygidium, non-fulcrate thoracic segments, and a trilobite-like arrangement of cephalic limbs (Fortey *in* Kaesler 1997). Although this fairly small number of species are probably undeserving of the taxonomic status of a class, they probably constitute a sister group to the Trilobita (Fortey *in* Kaesler 1997; but see Edgecombe & Ramsköld (1999) for a contrary view). However, the Naraoiidae must be excluded from the Trilobita *sensu stricto*, if the latter is to be formally-defined based upon characters of solely calcified forms (Edgecombe & Ramsköld 1999; Hou & Bergstrøm 1997).

(2) The suggestion that the olenellids, long regarded as trilobite taxa, are more closely-related to the Chelicerata by Lauterbach (1980, 1983) (thus making the Trilobita paraphyletic) generated a detailed study into the definition of Trilobita (Fortey & Whittington 1989). Lauterbach argued that the similarities between the olenellids and trilobites are due to symplesiomorphy (those characters inherited from a more distant ancestor than from the most-recent common ancestor of the group). This assertion has been strongly countered (Fortey & Whittington 1989; Ramsköld &

Edgecombe 1991; Edgecombe & Ramsköld 1999) and the issue of trilobite monophyly is now well accepted.

(3) The status of the order Agnostida Salter, 1864 as trilobites has been questioned. Agnostids are minute, have only two or three thoracic segments, and have a pygidium that closely matches the cephalon in outline (Whittington *et al. in* Kaesler 1997). No protaspid stages have ever been found. However, the appendages of a member of the suborder Agnostina, are known in exquisite detail from immature phospatized material from the Upper Cambrian 'Orsten' faunas of Sweden (Müller & Waloszek 1987). The Agnostina share some apomorphies with the Eodiscina (Jell 1975; Fortey 1990; Zhang *et al.* 1980), an undisputed trilobite suborder. However, due to the former taxon's many autapomorphies, it has been argued that agnostids should not be placed within the Trilobita (Resser 1938) and that the similarities between the Agnostina and Eodiscina are merely convergences (Ramsköld & Edgecombe 1991; Shergold 1991). One line of evidence that is cited in support of this view is the discovery of a calcified eodiscoid protaspis (Shergold 1991). As no calcified protaspid stages have been found for Agnostina, this discovery seemingly demonstrated a closer relationship of the Eodiscina to the more typical trilobites; implying that the Agnostina is independently derived. However, it is equally possible that the non-calcification of the agnostid protaspis is secondarily derived, perhaps a consequence of progenesis, and the Eodiscoidea and Agnostina are sister groups within the Trilobita (Fortey & Theron 1994). Recent cladistic analyses have, indeed, placed the Agnostina firmly within the Trilobita (albeit in an uncertain position within the class; but see that of Edgecombe & Ramsköld 1991, which places the agnostids as a sister group of restricted Trilobita). High-level phylogenetic studies have placed it as the basal sister group to the clade of other trilobite lineages (Wills *et al.* 1994, 1998) or as sister group to the Eodiscina, these clades then being the sister group to the other trilobite lineages (Fortey & Theron 1994, text-fig. 7). However, when one character in the latter study was re-coded (the rostral plate of agnostids being secondarily lost rather than absent) the Agnostina-Eodiscina clade was resolved as highly derived within the higher Trilobita (Fortey & Theron 1994, text-fig. 8; but see Smith (1994, p. 37) for reasons why this method is undesirable). A lower level study resolved it as the sister group to the suborder Eodiscina, this clade being basal sister group to the non-olenelloid trilobites (Fortey 1990, text-fig. 14). It may seem strange that their

phylogenetic position is so inconsistent within analyses, even though the limbs of Agnostina have been described in such detail. However, not all the fossil groups that are included in the conducted studies have full information available; for example, no limbs are known for Eodiscina. What new information may help to resolve the issue of the phylogenetic position of Agnostina? Detail of their ventral morphology would be invaluable. If olenellid-like rostral plates (i.e. with a perrostral suture) are discovered in agnostids or eodiscoids, then the inclusion of the Agnostida into the higher Trilobita would be further supported. The discovery of early ontogenetic stages of 'conventional' trilobites with agnostid-like limbs would give support to the idea that the agnostids arose by progenesis (achieving sexual maturity at an 'arrested' stage of ontogenetic development) (Fortey 2001).

1.3.2 Who makes up the group and what other cladistic studies have there been?

Despite all the work on unifying the group, the number of constituent orders still remains unstable: Harpetida was recently split from the Ptychopariida (Ebach & McNamara 2002). The orders unequivocally placed within Trilobita are presently:

- Redlichiida
- Ptychopariida
- Asaphida
- Harpetida
- Proetida
- Phacopida
- Lichida; and
- Corynexochida

Even so, there is still great contention regarding interordinal and intraordinal relationships. Figure 1.4 offers a cautious portrayal of overall trilobite relationships.

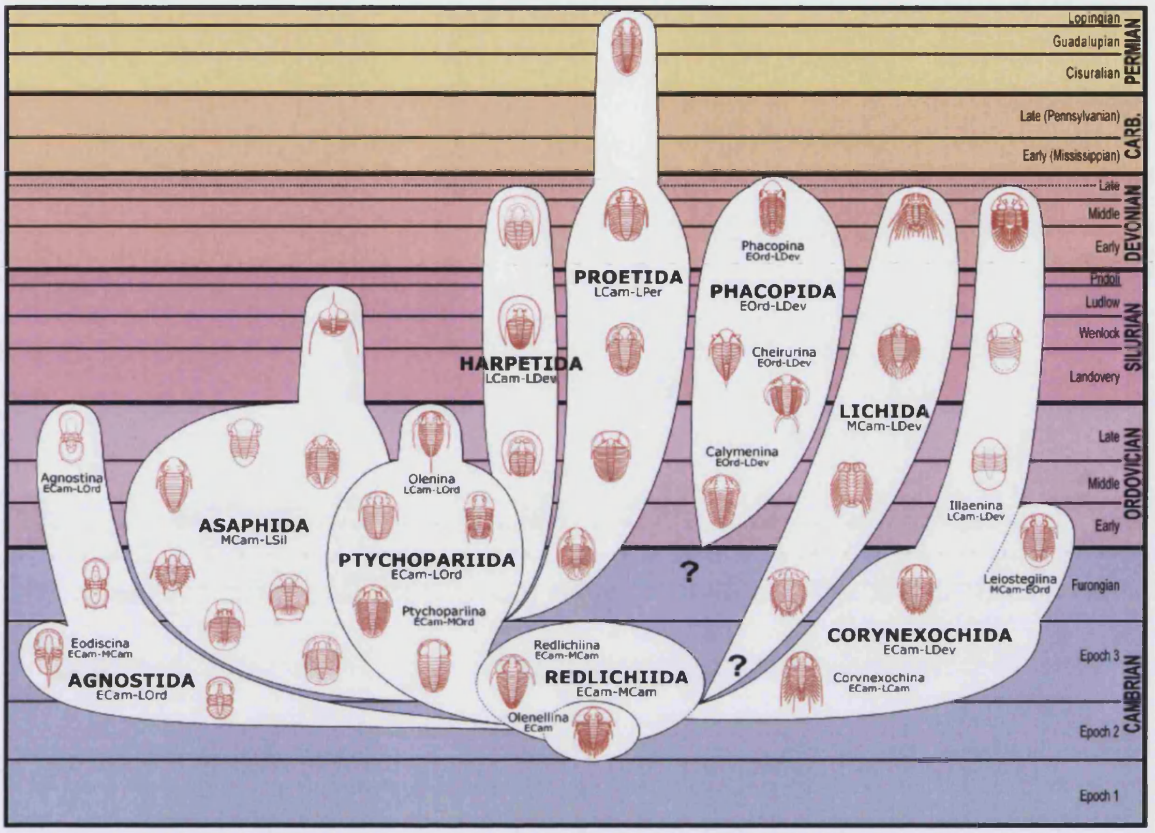

Figure 1.4: Putative trilobite ordinal relationships (http://www.trilobites.info/triloclass.htm).

1.3.2.1 Order Redlichiida

Suborder Redlichiina Richter, 1932. This taxon has been reviewed in depth (Zhang *et al. in* Kaesler 1997) but the suborder has not been subjected to rigorous phylogenetic analyses. The suborder is characterised by an opisthoparian facial suture, and a rostral plate that is transversely narrower than in Olenellina and that is bounded by rostral and connective sutures, amongst other features (Zhang *et al. in* Kaesler 1997). However, it is difficult to diagnosis this suborder soundly because it is probably paraphyletic; ptychoparioid, corynexochid and possibly other trilobite taxa have sister groups that would be currently classified in the Redlichiina (Fortey 2001).

This suborder consists of three superfamilies: (1) the Emuelloidea Pocock, 1970, (2) the Redlichoidea Poulsen, 1927, and (3) the Paradoxidoidea Hawle and Corda, 1847. These comprise one, twelve and two families respectively. It is likely that

the Redlichiina occupies a most basal position within the non-olenelloid trilobites (Fortey 1990, 2001).

Suborder Olenellina Walcott, 1890. Representatives of this suborder include the first trilobites to appear in the fossil record (Lieberman 1998) and the Olenellina is widely thought to be the basal trilobite clade (Fortey 1990; Fortey & Owens *in* Kaesler 1997; Fortey & Whittington 1989; Ramsköld & Edgecombe 1991). This taxon is a major, morphologically diverse group of trilobites that is characterised by the primary lack of facial sutures, a transversely wide rostral plate that extends between the genal angles, and a nonfulcrate thorax, among other features (Palmer & Repina *in* Kaesler 1997).

The possibility of a close phylogenetic relationship between some olenelloids and limuloids has been mentioned above. Although this hypothesis has been refuted, the possibility of Olenellina being paraphyletic with respect to the Redlichiina remains (Budd 1995; Fortey & Whittington 1989; Palmer & Repina 1993; Repina 1990).

This Olenellina has, until recently, been thought to comprise two superfamilies: (1) the Olenelloidea Walcott, 1890, and (2) the Fallotaspidoidea Hupé, 1953 (Palmer & Repina *in* Kaesler 1997). However, recent phylogenetic analyses, on the suprafamilial, the generic and the species levels (Lieberman 2001, 1998 and 1999 respectively) have yielded a different taxonomic classification. The generic level analysis resulted in the division of the suborder into *three* superfamilies - the Olenelloidea Walcott, 1890, the Judomioidea Repina, 1979, and the Nevadioidea Hupé, 1953 - and the removal of the superfamily Fallotaspidoidea Hupé, 1953 in order to avoid making the suborder paraphyletic (Lieberman 1998).

The Fallotaspidoidea was removed because it may share a more recent common ancestry with the Redlichiina Richter, 1932 than it does with other members of the Olenellina (Lieberman 1998). It is also putatively paraphyletic and, therefore, should be referred to informally as the 'fallotaspidoids' (Lieberman 1998; see Wiley 1979 for the within-quotes convention for paraphyletic groups). A higher phylogenetic analysis based on the three superfamilies Olenelloidea, Judomioidea and Nevadioidea showed that the Olenelloidea, along with the genus *Gabriellus* Fritz 1992, are the sister group of the Judomioidea Repina, 1979 (Lieberman 2001). The 'Nevadioidea' Hupé, 1953 were shown to be paraphyletic (Leiberman 2001).

1.3.2.2 Order 'Ptychopariida' Swinnerton, 1915, emend. *Fortey 1990*

This taxon is notoriously problematic. It contains two definite suborders: (1) the Ptychopariina Swinnerton, 1915 and (2) the Olenina Fortey, 1990. The Harpina Whittington, 1959 *in* Moore (1959) was assigned to this group prior to 2002 (when it was given ordinal status; see section 1.3.2.4).

The suborder Pychopariina is unequivocally paraphyletic, containing the primitive members of the subclass Libristoma that lack the synapomorphies of the more derived groups (Cotton 2001; Fortey 1990). Three ptychoparioid families have been subjected to cladistic analysis: (1) the Conocoryphidae Angelin, 1854 (Cotton 2001); (2) the Shumardiidae Lake, 1907 (Waisfield *et al.* 2001); and (3) the Alokistocaridae Resser, 1939 (Sundberg 1999). The first was found to be polyphyletic, one of its constituent families having been referred to the Corynexochida (Cotton 2001), and the two others are monophyla (Sundberg 1999, Waisfield *et al.* 2001).

The Olenina comprise an accepted monophyletic order (Fortey 1990; Henningsmoen 1957) and their ontogenies are well understood (e.g. Clarkson & Ahlberg 1997, 2002; Clarkson & Taylor 1995). Their phylogenetic relationships have been well described (e.g. Henningsmoen 1957; Westergård 1922). However, there has been no phylogenetic analyses conducted on this group; their phylogeny has been determined primarily from the direct 'reading' of the stratigraphic record because their record in the Upper Cambrian 'olenidskiffer' is unusually continuous (Fortey 1990; Clarkson *et al.* 1998). The suborder Olenina consists of only one family, the Olenidae Burmeister, 1843. There have been some attempts to incorporate other families into the Olenina (e.g. Palmer 1965; Shergold 1980), but many of these shared characters emphasised are symplesiomorphic or homoplasious (Fortey 1990).

1.3.2.3 Order Asaphida Salter, 1864, emend. *Fortey and Chatterton, 1988*

This large clade has been thoroughly reviewed and subjected to a cladistic analysis (Fortey & Chatterton 1988). This was one of the first applications of cladistics to a entirely extinct group (Fortey 2001). Members of the group are united by presence of the ventral medial suture (Fortey 2001; Fortey & Chatterton 1988). This may have arisen by reduction and eventual loss of the rostral plate (Chatterton *et al.* 1994; Fortey *in*

Kaesler 1997) and is secondarily lost by ankylosis (connection) in some groups, e.g. the Nileidae.

One group, the superfamily Anomocaroidea, is known to be paraphyletic with respect to the 'higher' asaphid taxa (Fortey *in* Kaesler 1997; Fortey & Chatterton 1988). This superfamily includes a number of primitive asaphid families that retain the natant hypostomal condition (Fortey 1990; Fortey & Chatterton 1988) but it may be possible to link these families with the more derived groups through further analysis (Fortey 1990). The derived groups are monophyletic (e.g. Nileidae, see Fortey & Chatterton 1988).

Another superfamily, the Trinucleoidea, has been particularly problematic to place. Whilst it almost certainly represents a monophyletic group (the convex and pyriform glabella being one uniting character) its relationship to other trilobite groups has been contentious. It has been previously classified with the ptychoparioids (Moore 1959), based on the presence of opisthoparian sutures in the least derived forms, but has recently been regarded as a superfamily of the Asaphida (Fortey & Chatterton 1988). This latter proposal is supported by several synapomorphies: (1) the resemblance of trinucleoid protaspides to the asaphoid protaspis; (2) the presence of a pre-occipital glabellar tubercle; (3) the existence of forms close to the Cambrian-Ordovician boundary that are morphologically intergrading; and (4) the identification of a reasonable candidate for the Cambrian sister group (Liostracinidae) that has a ventral median suture (Fortey & Chatterton 1988).

A morphocline analysis, incorporating adult and larval morphological characters, resolved the Trinucleoidea as basal sister group to the polyphyletic 'Anomocaroidea' and 'higher' Asaphida groups (Chatterton *et al.* 1994). There have, unfortunately, been few ontogenetic studies on this trilobite order and even fewer phylogenetic analyses on its constituent families.

1.3.2.4 Order Harpetida

This group has an unusual cephalic feature: the preglabellar area is long and there is often a characteristic brim surrounding the cephalon. Its similarity to the ptychoparioid family Norwoodiidae is convergent (Ebach & McNamara 2002). No cladistic analyses have been conducted on this group to date.

1.3.2.5 Order Proetida Fortey and Owens, 1975

This order contains all the stratigraphically youngest trilobites (Fortey 2001). It contains three main superfamilies: the Proetoidea, Aulacopleuroidea and the Bathyuroidea (Fortey *in* Kaesler 1997).

Whether or not the order is monophyletic or polyphyletic has been much debated. Support for monophyly derives from similarity in the protaspid stages. Shared characters include the very early development of a preglabellar field and an 'adult-like' body plan (Chatterton & Speyer *in* Kaesler 1997). It has been thought that the group derived from the subfamily Hystricurinae (Fortey & Owens 1975; Fortey 2001).

However, hystricurid larvae appear to have two morphotypes. One has small growth stages with transglabellar furrows, a re-entrant posterior margin and smooth protaspid and early meraspid stages (*'Paraplethopeltis'* and *Hyperbolochilus*), the other has a distinct pattern of regularly distributed tubercles and spines (e.g. the larvae of *Hystricurus*, *Parahystricurus* and *Amblycranium* (Lee & Chatterton 1997a). The recognition of two informal groups of larval morphology has led some workers to suggest the existence of two hystricurid lineages, each of which is ancestral to a different proetide group (Bergstrøm 1977; Lee & Chatterton 1997a). This renders the Hystricuridae as a basal paraphyletic group (Fortey 1989).

The close phylogenetic relationship between the hystricurids, dimeropygids, and the otarionines (aulacopleurids) is supported by the larval similarities of the two families (Adrain & Chatterton 1995; Chatterton 1994; Lee & Chatterton 1997a).

This order has been subject to a fair number of phylogenetic analyses. One cladistic analysis have been conducted on the superfamily Proetoidea: on the genus *Stenoblepharum* Owens, 1973 (Edgecombe *et al.* 1997). This genus is monophyletic and well resolved (Edgecombe *et al.* 1997).

Two cladistic analyses have been conducted on the superfamily Aulacopleuroidea:

(1) The genus *Otarion* Zenker, 1833 (Adrain & Chatterton 1994). *Otarion* was classified with other genera into a subfamily Otarioninae Richter & Richter, 1926. The morphological similarity between the type species of *Otarion* and that of *Aulacopleura* was found to be due to convergence. Whilst the tribe Otarionini Richter & Richter, 1926 was monophyletic, the Delorme Range species did not

form a clade excluding all other species and, hence, there was no evidence of a phyletic lineage linking these species (Adrain & Chatterton 1994); and

(2) The brachymetopid trilobite *Cordania* Clarke, 1892. This monophyletic group probably originated in the northern part of the Appalachian Province (Ebach & Edgecombe 1999).

Three cladistic analyses have been conducted on the superfamily Bathyuroidea:

(1) The two genera *Dimeropyge* Öpik, 1937, and the *Ischyrotoma* Raymond, 1925 (Chatterton 1994). Both were found to be monophyletic, *Ischyrotoma* being the basal sister group to *Dimeropyge* (Chatterton 1994) as suggested by Fortey & Owens (1975, p. 228);

(2) The 'Ischyrotoma group' within the family Dimeropygidae (the genera *Dimeropygiella*, *Ischyrotoma* and *Pseudohystricurus*) (Adrain *et al.* 2001). *Dimeropygiella* and *Ischyrotoma* were considered synonymous (Whittington 1963), but this analysis reveals that each is, in fact, a well supported clade (Adrain *et al.* 2001); and

(3) The families Dimeropygidae Hupé, 1953, and Toernquistiidae Hupé, 1953 (Chatterton *et al.* 1998). These were both monophyletic, but it proved difficult to unite them into a monophyletic group that excluded other proetides, e.g. some hystricurids were more closely allied to the dimeropygids and some were more closely allied to the toernquistiids (Chatterton *et al.* 1998).

Many detailed ontogenetic studies of this order are also available, e.g. Telephinidae (Chatterton 1980; Chatterton *et al.* 1999; Lee & Chatterton 1997b), Dimeropygidae (Chatterton 1980; Speyer & Chatterton 1989; Tripp & Evitt 1983).

1.3.2.6 Order Phacopida Salter, 1864

This massive taxon comprises three sub-orders: Calymenina, Cheirurina, and Phacopina (Fortey *in* Kaesler 1997). They share many possible synapomorphies, e.g. their distinctive protaspis (see Fortey 1990; Henningsmoen *in* Moore 1959).

Several phylogenetic analyses have been conducted on the Calymenina:

(1) A comprehensive cladistic analysis on the whole of the Calymenina, using protaspid larvae morphology (Chatterton *et al.* 1990). At least one representative

of the Calymenina, Cheirurina, Phacopida, Lichida, Odontopleurida, Proetida and Pychopariida trilobite orders was included. The 'Cheirurina' was shown to be paraphyletic, with some encrinurids sharing more similarities with members of the Phacopina than Cheiruridae, and the Calymenina was the basal phacopid sister group (Chatterton *et al.* 1990). This overall relationship within the Phacopida is supported by the cladistic analysis of Fortey (1990; figure 13).

(2) A cladistic analysis of the genus *Alcymene* n. gen. (Calymenidae; Ramsköld *et al.* 1994); and

(3) A cladistic analysis of the Reedocalymeninae (Calymenidae) was undertaken in order to provide a basis for biogeographic analysis (Turvey 2002).

The sub-order Phacopina has not been subjected to many cladistic analyses. However, there has been:

(1) A comprehensive analysis on the subfamily Phacopinae (Phacopida; Ramsköld & Werdelin 1991). Two major clades were found: one including species referred to *Acernaspis* and one including those referred to *Ananaspis*, *Paciphacops*, *Viaphacops*, and *Phacops*; and

(2) Two analyses on the family Calmoniidae Delo, 1935. The '*Malvinella* group' and the '*Metacryphaeus* group' were examined with cladistic analysis (Lieberman *et al.* 1991; Lieberman 1993 respectively). Both of these analyses were used to form a basis for classification of the constituent taxa.

The family Encrinuridae (Cheirurina) has been the focus of recent detailed morphological study (e.g. Edgecombe & Ramsköld 1992; Gass *et al.* 1992; Tripp *et al.* 1977). It has also been the subject of several cladistic analyses:

(1) The genus '*Encrinuroides*' Reed, 1931 (Edgecombe & Chatterton 1992; Edgecombe *et al.* 1998). The former analysis showed that '*Encrinuroides*' is paraphyletic with respect to the *Curriella* and *Encrinurus* plexi (Edgecombe & Chatterton 1992). The latter analysis demonstrated the ambiguity of the monophyly of the genera *Platycalymene* Shirley, 1936 and *Frencrinuroides* Lespérance & Desbiens, 1995 (Edgecombe *et al.* 1998);

(2) The genus *Distyrax* Lane, 1988 has been shown to be monophyletic (Edgecombe & Chatterton 1992);

(3) The superfamily Cheiruroidea (Edgecombe *et al.* 1988). The relationships between this subfamily and allied taxa were investigated using protaspid larvae and early developmental characters. The Pliomeridae was the basal sister group to the Staurocephalidae and the Encrinurinae, the latter group being the most derived (Edgecombe *et al.* 1988); and

(4) The subfamily Acanthoparyphinae Whittington & Evitt, 1954 (Adrain 1998). Five of the included genera (*Acanthoparypha* Whittington & Evitt, 1954; *Hyrokybe* Lane, 1972; *Pandaspinapyga* Esker & Levin, 1964; *Parayoungia* Chatterton & Perry, 1984; and *Youngia* Lindström, 1885) form a monophyletic group and is supported by several synapomorphic character states (Adrain 1998). However, when the group was expanded to include *Holia* Bradley, 1930 an effective subfamilial diagnosis became more difficult (Adrian 1998).

Apart from the analysis by Edgecombe *et al.* (1988) very little, if any, ontogenetic data were incorporated into these studies.

1.3.2.7 Order Lichida (Fortey in *Kaesler, 1997)*

The order Lichida is considered to include three superfamilies: Lichoidea, Odontopleuroidea and Dameselloidea (Fortey *in* Kaesler 1997).

Whether the subfamilies Lichoidea and the Odontopleuroidea should be placed into the same order, Lichida, has been strongly debated. Fundamental similarities between the protaspides of the two groups, and the putative homology of their glabellar lobes, argue for their monophyly (Fortey 1990; Fortey *in* Kaesler 1997; Henningsmoen 1957; Thomas & Holloway 1988). However, study of their ventral surfaces gives reason to doubt this close relationship (Whittington 2002).

In addition, there has been some suggestion of a close relationship between Lichidae and Styginidae (of the order Corynexochida) (an idea originating with Beecher 1897 and supported by Thomas and Holloway (1988, p. 245) and Fortey (in Kaesler, 1997, p. 299)) but other studies suggest that this is questionable (Whittington 1999, 2002).

Only one phylogenetic analysis has been conducted on the family Lichidae. A subfamily of the lichids, Trochuriae Phleger, 1936, comprises two main clades (Adrain 1994). One clade includes those trilobites that were fairly common in the Silurian and

underwent a huge radiation in the Early Devonian. The Silurian members of this clade have been classified into a paraphyletic group, the subgenus *Acanthopyge* (*Lobopyge*) Přibyl & Erben, 1952 (Adrain 1994; Thomas & Holloway 1988). A cladistic analysis of this taxon has been undertaken (Ebach & Ahyong 2001).

There have been several phylogenetic analyses on the family Odontopleuridae Burmeister, 1843:

(1) A cladistic analysis of the subfamilies Selenopeltinae Hawle & Corda, 1847, and Ceratocelphalinae Richter & Richter, 1925, emended by Prantl & Přibyl (1949) (Ramsköld 1991a);

(2) A cladistic analysis of the odontopleurid subfamily Koneprusiinae Vanêk and Pek, 1987 (Ramsköld 1991b). The genera *Koneprusia* and *Laethoprusia* are found to be monophyletic; the latter being the most derived genus of the subfamily (Ramsköld 1991b);

(3) A phylogenetic analysis of the polyphyletic odontopleurid trilobite genus *Leonaspis* Richter & Richter, 1917 (Ramsköld & Chatterton 1991). Three conclusions resulted: (1) A much-restricted monophyletic group including the type species is endemic to Siluro-Devonian Gondwanaland; (2) that several species traditionally assigned to *Leonaspis* actually belong to the subfamily Acidaspidinae, for which the new genus *Exallaspis* was proposed; and (3) that the majority of species traditionally assigned to *Leonaspis* should be assigned to *Kettneraspis*. Four groups of equal rank were discovered;

(4) A phylogenetic analysis of the genera *Ceratocara* Ramsköld, 1991a, and *Ceratocephala* Warder, 1838 (Chatterton *et al.* 1997). Both are monophyletic and the relationships within *Ceratocara* are particularly stable (Chatterton *et al.* 1997); and

(5) A cladistic analysis of the genus *Odontopleura* Emmrich, 1839 (Adrain & Chatterton 1990).

1.3.2.8 Order Corynexochida Kobayashi, 1935

Three suborders are included in this order: Corynexochina, Illaenina, and Leiostegiina (Fortey *in* Kaesler 1997). Illaenina and Leiostegiina have not always been included in the Corynexochida but are at present (Fortey 1990; Lane & Thomas 1983;

Přibyl & Vaněk 1971): this extends the stratigraphic range of the Cambrian Corynexochida into the Devonian (Fortey 1990). All three taxa show the conterminant hypostome condition and a distinctive pestle-shaped glabella with splayed glabellar furrows (Fortey 1990). The latter character is typical of the early life stages of other trilobite orders and there has been some suggestion that its presence in the adult corynexochids is neotenous (Fortey *in* Kaesler 1997; Robison 1967). However, if this is the case, it should be recognised that this heterochronic transformation may occur more than once and that the Corynexochida may, therefore, be polyphyletic (Fortey *in* Kaesler 1997).

In addition, the family Illaenidae (suborder Illaenina) seems to differ from the Styginidae (of the same suborder; Whittington 1999) and, according to Whittington, shares some key characters with the asaphid trilobite family Nileidae (Whittington 2000).

There have been very few cladistic analyses of corynexochid taxa. None have focused on the inter-relationships between the suborders. One was conducted on the subfamily Oryctocephalinae Beecher, 1897 (Sundberg & McCollum 1997). Four groups of taxa were recovered: (1) the outgroup (*Lancastria roddyi*); (2) an *Oryctocephalus* group; (3) a stem group at the base of the *Oryctocephalites*; and (4) an *Oryctocephalites* group (Sundberg & McCollum 1997). This grouping prompted emended diagnoses of the genera involved.

1.4 CHARACTERS AND THEIR SELECTION

Sister-groups are discovered by identifying apomorphic characters inferred to have originated in their most recent common ancestor and shared by its descendents. These shared apomorphies, or synapomorphies, can be thought of as evolutionary homologies: that is, structures inherited from the most recent common ancestor.

Cladistic analysis order synapomorphies into a nested hierarchy by choosing the arrangement of taxa that accounts for the greatest number of characters in the simplest way (or *parsimonious* way; parsimony is simply the most robust criterion for choosing between solutions: it is not a statement about how evolution may or may not have taken place). Thus, operations of cladistic analysis are strongly influenced by the selection and resolution of taxa and characters.

Computerized cladistic analysis renders variation into discrete codes and so often needs qualitative characters. Continuous and quantitative characters can be

coded, if deemed useful, by measuring a character state *in relation* to another (Thiele 1993).

Previous literature (phylogenetic analysis and careful taxonomic work) were searched thoroughly to elucidate important characters. Any perceived difference in characters was noted and all were initially selected to provide structure to the dataset; the old adage: rubbish-in, rubbish-out. Inconsistencies were discovered within character states over time: these were discarded and the dataset was condensed and purified. The work of previous workers was, needlesstosay, absolutely invaluable during this period and much of the character selection stage was built upon their knowledge. I added to this foundation with new characters found by careful and detailed morphological study of the literature and many specimens. The characters noted in this thesis are attributed to other workers, where needs be, but most represent previous knowledge consolidated with that gleaned through fresh eyes.

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SYSTEMATICS OF THE TRILOBITE FAMILIES LICHIDAE HAWLE & CORDA, 1847 AND LICHAKEPHALIDAE TRIPP, 1957: THE APPLICATION OF BAYESIAN INFERENCE TO MORPHOLOGICAL DATA

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SYNOPSIS The first cladistic and Bayesian analyses of the trilobite families Lichidae Hawle & Corda, 1847 and Lichakepalidae Tripp, 1957 are presented. Thirty-one lichid genera and five lichakephalid outgroup taxa were coded for 48 characters using published descriptions. Two methods of phylogenetic inference were adopted: (1) a maximum-parsimony (MP) approach and, for the first time in a palaeontological context, (2) a Bayesian inference (BI) approach. The consensus trees from the MP and BI analyses were topologically similar, but differed principally in the deeper branches (i.e. the relationships between major clades). The Lichidae is monophyletic with respect to the Lichakephalidae in both analyses. The Trochurinae (Thomas & Holloway, 1988) is well supported by both analyses. Other groups are also supported (i.e. Tetralichinae, Echinolichinae and Platylichinae); two, however, are not (i.e. Homolichinae and Lichinae). A classification is proposed that represents the main branching pattern of the MP tree and also incorporates many elements of the BI tree, whilst applying least violence to the existing usage of the taxa. The Lichinae as defined here consists, therefore, of four main groups and these are given tribal status: Echinolichini, Tetralichini, Platylichini and Dicranopeltini. The last taxon is re-erected to contain those taxa formerly placed in the subfamily Lichinae. *Lichas* is assigned to a monogeneric tribe, the Lichini.

KEY WORDS Bayesian, cladistics, Lichidae, morphology, phylogenetics, Trilobita

Contents

INTRODUCTION

There are, at present, nearly 180 recognised families within the class Trilobita (see Jell & Adrain 2003). Somewhat surprisingly, though, only some 50 cladistic analyses have been conducted on the group. Furthermore, out of these, only around 12 have aimed to resolve trilobite phylogenetic relationships at the familial-level or higher (i.e. Fortey & Chatterton 1988; Ramsköld 1991; Babcock 1994; Sundberg & McCollum 1997; Chatterton *et al.* 1998; Lieberman 1998, 2001; Sundberg 1999; Cotton 2001; Waisfield *et al.* 2001; Ebbestad & Budd 2002).

It is recognised, then, that there remains much to be known about trilobite phylogenetic relationships at a high taxonomic level and, hence, this study focuses on the phylogenetic relationships of the superfamily Lichoidea *sensu* Fortey (Fortey *in* Kaesler 1997), as a basis for the revised *Treatise on Invertebrate Paleontology, Trilobita.*

The Lichoidea has been the subject of a detailed and comprehensive study by Thomas & Holloway (1988) and this review has contributed greatly to the present work. Possible relationships within the Lichoidea (and also the relationships of these taxa with other trilobite groups) were considered by Thomas & Holloway (1988), but phylogenetic analyses of all genera have never been attempted. The lichid genera *Acanthopyge (Lobopyge)* Pribyl & Erben, 1952 and *Borealarges* Adrain, 1994 have been the subject of species-level cladistic analyses (Ebach & Ahyong 2001 and Adrain, 2003, respectively), as has *Hemiarges* Gürich, 1901 (Rudkin *et al.* 1994).

The superfamily Lichoidea is considered to be a monophyletic group supported by the unique lobation of the glabella. It comprises two families: the Lichidae Hawle & Corda, 1847 and the Lichakephalidae Tripp, 1957. Thomas & Holloway (1988) recognised five subfamilies within the Lichidae: Lichinae Hawle & Corda, 1847, Echinolichinae Phleger, 1936, Homolichinae Phleger, 1936, Tetralichinae Phleger, 1936 and Trochurinae Phleger, 1936. A subsequent review, in the light of new data, by Holloway & Thomas (2002), saw the re-assignment of the genus *Metopolichas* Gürich, 1901 to the Lichinae from the Homolichinae. Similarly, the genera *Platylichas (Platylichas)* Gürich, 1901, *Platylichas (Rontrippia)* Thomas & Holloway, 1988, *Allolichas* Krueger, 1992, *Autoloxolichas* Phleger, 1936 and the poorly-known *Metalichas* Reed, 1902 were all assigned to the subfamily Platylichinae Phleger, 1936 (Holloway & Thomas 2002: see Table 1 for the previous lichoid classification after Thomas & Holloway (1988) and Holloway & Thomas (2002)).

Several species of the lichid genera *Borealarges* Adrain, 1994 and *Dicranogmus* Hawle & Corda, 1847 have been described in detail using superbly preserved material from localities in the Canadian Arctic Archipelago (Adrain 1994, 2003, respectively). A restricted definition of *Richterarges* Phleger, 1936 is given within the former paper; some species hitherto placed in *Richterarges* were assigned to the genus *Borealarges.*

Traditionally, the method of morphological character-based parsimony analysis has been used to investigate phylogenetic relationships between fossil taxa; other approaches, such as maximum likelihood and Bayesian inference (BI), dealt only with molecular data. However, recent new stochastic models have been developed to handle morphological data (e.g. BI: Huelsenbeck & Ronquist 2001). The BI method may be particularly attractive to palaeontologists: it is extremely computationally efficient and allows large datasets, including those with large amounts of missing data, to be analysed quickly whilst sampling lots of trees (Ronquist 2004). BI has been applied to a heterogeneous dataset (consisting of morphological and nucleotide data; Nylander *et al.* 2004). However, although it has previously been put into a palaeontological context (see Budd 2004), it has never before been applied explicitly to fossil taxa.

BI has a strong connection to the maximum likelihood method (Felsenstein 1981) and evaluates the BI posterior probability of a tree given the character matrix, a model of evolutionary change and a set of, so-called, 'priors'. For morphological data, the prior assumes that character states are present in equal frequency in the dataset. The posterior probability for a hypothesis is proportional to the likelihood multiplied by the prior probability of that hypothesis (the probability of the hypothesis without reference to the available data). The optimal hypothesis is that which maximises the posterior probability (see Holder & Lewis 2003).

BI combines the advantages of defining an explicit probability model of character evolution and of obtaining a rapid approximation of posterior probabilities of trees through the use of the Markov chain Monte Carlo (MCMC)

Table 1 A list of lichoid taxa presented in the classification system of Thomas & Holloway (1988) and Holloway & Thomas (2002).

Family Lichidae Moore, 1959
- Subfamily Lichinae Hawle & Corda, 1847
  - *Lichas* Dalman, 1827
  - *Arctinurus* Castelnau, 1843
  - *Dicranopeltis* Hawle & Corda, 1847
  - *Oinochoe* Thomas & Holloway, 1988
  - *Pseudotupolichas* Phleger, 1936
  - *Uralichas* Delgado, 1892
  - *Metopolichas* Gurich, 1901
- Subfamily Echinolichinae Phleger, 1936
  - *Echinolichas* Gurich, 1901
  - *Terataspis* Hall, 1863
- Subfamily Homolichinae Phleger, 1936
  - *Conolichas* Dames, 1877
  - *Hoplolichas* Dames, 1877
  - *Hoplolichoides* Phleger, 1936
  - *Leiolichas* Schmidt, 1885
  - *Otarozoum* Thomas & Holloway, 1988
- Subfamily Tetralichinae Phleger, 1936
  - *Amphilichas* Raymond, 1905
  - *Apatolichas*, Whittington, 1963
  - *Lyralichas* Weber, 1948
- Subfamily Trochurinae Phleger, 1936
  - *Trochurus* Beyrich, 1845
  - *Acanthopyge* Hawle & Corda, 1847
  - *Akanthopyge* Phleger, 1936
  - *Ceratarges* Gurich, 1901
  - *Hemiarges* Gurich, 1901
  - *Radiolichas* Reed, 1923
  - *Richterarges* Phleger, 1936
  - *Uripes* Thomas & Holloway, 1988
  - *Borealarges* Adrain, 1994
- Subfamily Platylichinae Phleger, 1936
  - *Platylichas* (*Platylichas*) Gurich, 1901
  - *Platylichas* (*Rontrippia*) Thomas & Holloway, 1988
  - *Allolichas* Krueger, 1992
  - *Autoloxolichas* Phleger, 1936

approach (Metropolis *et al.* 1953; Hastings 1970). MCMC, or the Metropolis–Hastings algorithm (Hastings 1970), is a simulation technique that takes the form of a correlated random 'walk' through the parameter space; this can then, after some point in the sequence, approximate probability distribution by periodically sampling values (Lewis 2001).

METHODS

Figures and systematic descriptions were derived mainly from Thomas & Holloway (1988), Adrain (1994, 2003) and Holloway & Thomas (2002). These were used to code lichoid genera into a dataset (see Appendix). Forty of the 50 taxa described in Thomas & Holloway (1988) and Holloway & Thomas (2002) were initially coded using these texts; the remaining 10 taxa were either unfigured or very badly preserved. *Borealarges* was coded from Adrain (1994) and Thomas & Holloway (1988). Tripp (1957) was used to code some hypostomal characters and Whittington (2002) likewise for some thoracic characters.

If a character state was polymorphic for a given genus, this information was also included. There is no robust method for dealing with taxonomic polymorphism (where characters exhibit more than one state within a higher-level taxon while remaining fixed within species). One approach is to break polymorphic taxa down into monomorphic subunits representing lower-level taxa. However, this approach is undesirable because it increases the number of taxa in the analysis. Nixon & Davis (1991) showed that coding polymorphies as missing data could lead to erroneous topologies. Similarly, other methods can perform badly (Weins 1998). Polymorphic (or ambiguity) coding seems to perform moderately well (Weins 1998); this method was adopted as it allows us to be conservative with the number of taxa and, unlike other methods, avoids making assumptions about which character states are primitive (Simmons 2001). Indeed, many other phylogenetic studies code polymorphisms as such at a higher taxonomic level than species (see Kornet & Turner 1999). Polymorphism affects only a comparatively small part of the dataset (2.4%) and it is thought that it will not greatly bias the resulting phylogeny, if at all.

Datasets including taxa with large numbers of equivocal or missing codings often yield large numbers of most parsimonious trees (MPTs). Small numbers of taxa containing large amounts of missing codings can often frustrate resolution by being highly mobile over large proportions of the topology. Although the proportion of missing entries in the matrix is 26%, some species had as many as 88% of their entries missing (i.e. *Gaspelichas*). However, any taxon that does not have a unique set of character states can be safely deleted without affecting the most parsimonious interpretation of the relationships between remaining taxa (Wilkinson 1995). In doing so, the number of most parsimonious trees produced from an analysis is often reduced. Hence, the program TAXEQ3 was run on the initial dataset in order to assess whether any taxa could safely be excluded from the analysis (Wilkinson 2001).

TAXEQ3 recognised *Acanthopyge*, *Akantharges*, *Ceratarges* and *Borealarges* as being potential equivalents to *Craspedarges* (asymmetric all one way), which would permit the deletion of the latter taxon from the analysis. However, it also recognised *Richterarges* (and *Terranovia*) as a potential equivalent to *Craspedarges* (asymmetric both ways); the latter, therefore, cannot be deleted from the analysis without the risk of the relationships between the remaining taxa being affected. Nevertheless, it was necessary to exclude the genera *Ceratolichas*, *Gaspelichas*, *Craspedarges* and *Terranovia* from the analysis: they vastly increased both the computing time of the analysis and the number of resulting MPTs because of the huge amounts of missing data. Two methods of tree estimation were adopted: (1) the more traditional maximum-parsimony (MP) approach and (2) the newer method of Bayesian inference (BI).

Maximum-parsimony analysis

The dataset was tested for significant non-random structure using the permutation tail probability (PTP) test (100 replicates with heuristic search via 100 random stepwise additions and TBR (tree bisection and reconnection) branch-swapping: Faith & Cranston 1991). The null hypothesis of this test is that 'the analysis of a comparable set of randomly covarying characters could produce a cladogram of equal, or even

shorter, length' (Kitching *et al.* 1998). The null hypothesis can be rejected if the *p*-value is less than, or equal to, 0.05. The PTP test ($P < 0.01$) indicated that there was significant non-random structure in the dataset; further analyses could then be conducted confidently.

The dataset (see Appendix) was analysed using PAUP (version 4.0b10*: Swofford 2002). All characters were unordered and equally weighted. For all runs of PAUP, heuristic searches were employed (via 100 random stepwise additions and TBR branch-swapping). Character states were reconstructed using the 'accelerated transformation optimisation' criterion (ACCTRAN). This option maximises homoplastic character changes that are represented as reversals rather than as parallelisms (Pinna 1991). Consequently, primary homologies are preserved as long as possible within the constraints of parsimony.

Bootstrap proportions (100 replicates with heuristic search via 10 random stepwise additions and TBR branch-swapping: Felsenstein 1985) were calculated to measure the frequency of a branch's occurrence in the resampling of pseudoreplicates from the dataset (and, thus, its strength of support). Branch support values (Bremer 1988, 1994) were calculated using TreeRot (Sorenson 1996). These provide a measure of relative support for each clade, i.e. the number of additional steps that are required before a clade is lost from the strict consensus tree of the minimum-length cladograms (Kitching *et al.* 1998).

Bayesian inference analysis

Phylogenetic analysis was also performed using BI (Larget & Simon 1999; Huelsenbeck *et al.* 2001). All analyses were conducted using the program MrBayes 3.0B4 (Huelsenbeck & Ronquist 2001). A default random tree was used as a starting point.

The MCMC procedure requires that, in order for the Markov chains to reach stationarity, the simulation is run for long enough and that the initial portion of the sequence is discarded: only then will the sampled tree topologies be arbitrarily close to their posterior probabilities (Larget & Simon 1999).

Four independent Markov chains (one cold chain and three incrementally heated chains) were run for 500 000 MCMC generations, with tree sampling every 10 generations. Both the priors for the model parameters and the parameters of the likelihood model were left as default (see command reference file for details: Huelsenbeck & Ronquist 2001).

To establish whether the Markov chains had reached stationarity, the likelihood scores of sampled trees were plotted against generation time using Tracer (Rambaut & Drummond 2003). Stationarity was said to have been reached when the likelihoods of the sample points reached a stable equilibrium (Huelsenbeck & Ronquist 2001). Trees generated prior to stationarity were discarded as 'burn-in' samples. In this analysis, the first 5000 sampled trees were ignored. A 50% majority-rule consensus tree (including other compatible groupings) was constructed from the remaining trees using PAUP, in order to calculate the *a posteriori* probability of each bipartition.

Finally, the morphological dataset was entered into MacClade Version 4.06 (Maddison & Maddison 2003) to investigate patterns of character evolution.

Outgroup

The Lichakephalidae Tripp, 1957 is used as the outgroup; it has been accepted as basal to the Lichidae by previous workers (e.g. Thomas & Holloway 1988: 247). The Lichakephalidae, as accepted by Thomas & Holloway (1988), contains the following taxa: *Lichakephalus* Sdzuy, 1955; *Acidaspidella* Rozova, 1963; *Eoacidaspis* Poletaeva, 1956; *Lichakephalina* Antcygin *in* Varganov *et al.*, 1973; *Acidaspidina* Lazarenko, 1960 and *Brutonia* Thomas & Holloway, 1988. The taxon *Brutonia* Thomas & Holloway, 1988 is not coded here because figures of the type species were not easily accessible.

Some workers accept the Lichakephalidae only when *Eoacidaspis* is excluded (the latter taxon being placed in the Eoacidaspididae: see Shergold *et al.* 2000). However, it has been proposed that the Lichakephalidae and Eoacidaspididae Poletaeva, 1957 are synonymous (Thomas & Holloway 1988). It was, therefore, decided to include *Eoacidaspis* (but see Systematic Palaeontology, below).

Characters

The terminology of Thomas & Holloway (1988) is followed throughout unless otherwise stated. Some lichid ontogenies are known: *Acanthopyge* (Whittington 1956; Chatterton 1971), *Amphilichas* (Hu 1974; Chatterton 1980; Tripp & Evitt 1981) and *Hemiarges* (Hu 1974; Chatterton 1980; Tripp & Evitt 1981; Speyer & Chatterton 1989). Characters of small growth stages were not coded into the dataset as the ontogenies of most coded taxa are, as yet, unknown. This was in order to minimise the proportion of missing data within the dataset, an attribute that may be detrimental to phylogenetic analyses (e.g. Platnick *et al.* 1991; Wilkinson 1995). However, known ontogenetic stages will be discussed later in the context of the resulting phylogeny (see Discussion). The terminology adopted here and lichoid morphological characters, are depicted in Figs 1 and 2. The character number in the following list corresponds directly to its number in the dataset (Table 2).

Cranidium

1. Sagittal length of the preglabellar field. States: 0, very narrow; 1, moderate; 2, accumulate, spatulate process. Outgroup: Lichakephalids have a moderate preglabellar field.
2. Posterior extent of longitudinal glabellar furrow. The longitudinal furrow, which arises from the posterior extension of the anterior lateral glabellar furrow, joins the adaxial ends of the posterior lateral glabellar furrows (see Fig. 3 for schematic illustrations of these character states). States: 0, joining only with S1 or axial furrow, not continuous with S0 (occipital furrow); 1, longitudinal glabellar furrow extends to S0 (may be weak posteriorly) and may conjoin with S1; 2, terminating at base of bullar lobe (hook-like); 3, extends only to S0, may be weak posteriorly; 4, effaced. Outgroup: In *Lichakephalus* and *Lichakephalina* the longitudinal furrow meets S1; these furrows are effaced in *Acidaspidella*, *Eoacidaspis* and *Acidaspidina*.
3. Path of S1. The first lateral glabellar furrow anterior to the occipital furrow is termed S1. This furrow varies in depth and direction. In lichakephalids it conjoins to S2 to circumscribe the lobe L2 (except in *Acidaspidina*, where L2 is not circumscribed by a conjoined S1 and S2

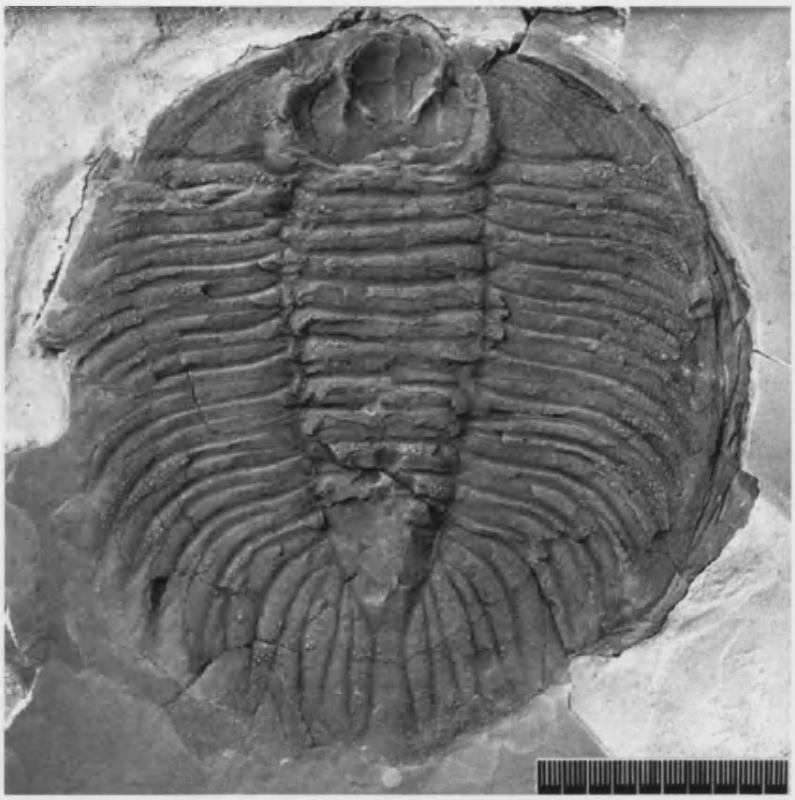

Figure 1 The holotype of the Silurian lichid, *Arctinurus boltoni* Bigsby, 1825. Scale bar = 5 cm.

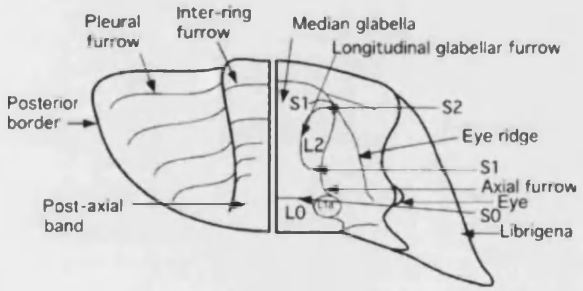

Figure 2 Labelled schematic illustration of a lichoid trilobite displaying the plesiomorphic condition (left half of the pygidium, right half of the cephalon). Lateral glabellar forrows are numbered from the posterior forward as S (sulcus), O (the occipital furrow) and then S1, S2 etc. Lateral glabellar lobes are numbered L (lobe), O (the lateral occipital lobe) and then L1, L2, etc.

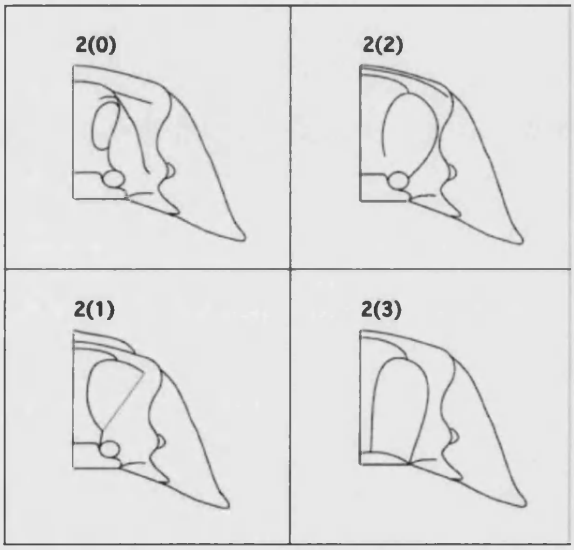

Figure 3 Schematic illustrations of the character states for character 2; character state 'effaced' is not shown.

(Thomas & Holloway 1988: 240). In some lichid taxa it is effaced, or almost so, whilst in other taxa it is deep and binds the bullar lobe posteriorly. In examples of the latter expression, S1 can variously impress across the median glabellar lobe (see Fig. 4 for schematic illustrations of these character states). States: 0, conjoins with S2 (as in *Lichakephalus*); 1, conjoins axial furrow and longitudinal furrow, weakly developed or only present on internal molds (as in *Hoplolichas*); 2, conjoins axial furrow and longitudinal furrow, deeply impressed (as in *Autoloxolichas*); 3, conjoins axial furrow and longitudinal furrow before posterolateral cranidial lobe; 4, conjoins axial furrow and longitudinal furrow before posterolateral cranidial lobe and continuous across width of glabella (as in *Trochurus*); 5, S1 absent. Outgroup: S1 of lichakephalids is deep and conjoins with S2.

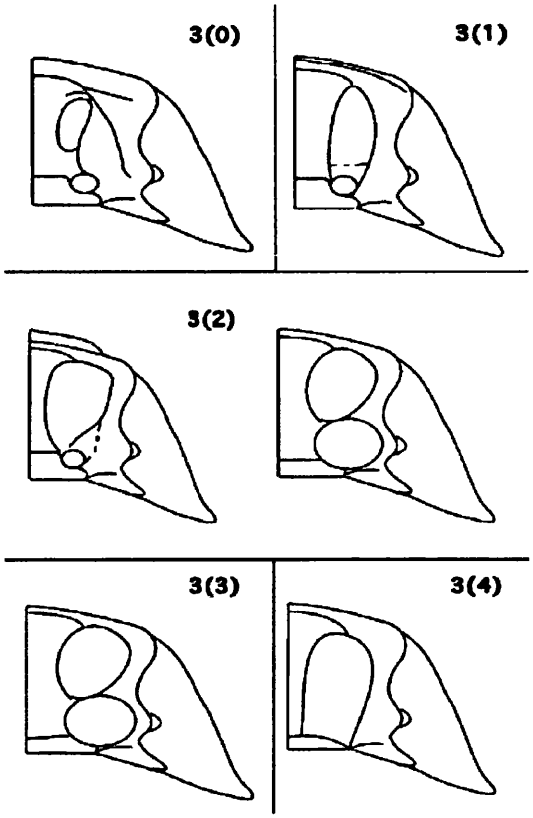

Figure 4 Schematic illustrations of the character states for character 3.

4. Path of axial furrow. The axial furrow outlines the axial region. In lichoids this is the furrow that bounds the L2, bullar or composite lateral lobes abaxially. The furrow that bounds the posterolateral lobe abaxially is not the axial furrow (Thomas & Holloway 1988: 189) (see Fig. 5 for schematic illustrations of these character states). States: 0, deep, running down to meet S0 or abaxial side of L1a (as in *Lichakephalus* and *Hoplolichas*); 1, posteriorly effaced (as in *Autoloxolichas*); 2, merging with S1 (as in *Lichakephalina*), sometimes expressed on the abaxial side of L1a (as in *Platylichas (Platylichas)*); 3, expressed on the adaxial side of the posterolateral cranidial lobe (as in *Akantharges*). Outgroup: All lichakephalids, except *Lichakephalina*, have the axial furrow running down to meet the abaxial side of L1a. The axial furrow of *Lichakephalina* merges with S1.
5. Width of median glabellar lobe. Variation in the width of the median glabellar lobe is measured as the ratio of its width at the anterior limits of the lateral glabellar lobes to either (1) its width at the juncture of the longitudinal furrows with S1/axial furrow, or (2) the ends of longitudinal furrows. States: 0, width anteriorly at least twice the width posteriorly; 1, width anteriorly greater than, but less than twice, the width posteriorly; 2, equal width anteriorly and posteriorly. Outgroup: *Lichakephalus*, *Eoacidaspis* and *Lichakephalina* have a large broad median lobe, whilst those of *Acidaspidella* and *Acidaspidina* are narrower.
6. Ornamentation of median glabella. States: 0, evenly scattered coarse tubercles; 1, a distinct single pair or row of paired larger tubercles (i.e. *Borealarges*); 2, fine granules/non-tuberculate; 3, pair of spines. Outgroup: *Lichakephalus* and *Acidaspidella* have coarse tubercles on the median glabella. All other lichakephalids have a non-tuberculate median glabella.
7. Anterior extent of the median glabella. States: 0, does not overhang the anterior border; 1, does overhang the anterior border. Outgroup: The median glabella of lichakephalids does not overhang anterior border.
8. Definition of glabellar lobe L1a. The most posterior lateral lobe is considered to be part of L1 and is subdivided into L1a and L1b (Whittington *in* Kaesler 1997: 7). Lobe L1a is the posterior lobe of the two and can be incorporated into a composite lateral lobe (e.g. *Amphilichas*;

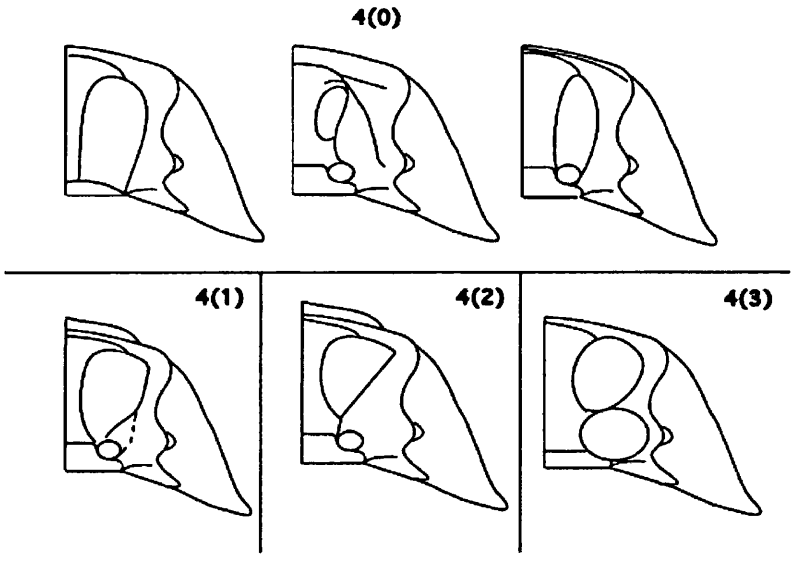

Figure 5 Schematic illustrations of the character states for character 4.

Thomas & Holloway 1988: fig. 246) or just simply lost (some members of *Dicranopeltis scabra* (Thomas & Holloway 1988: fig. 32)). States: 0, strongly; 1, weakly; 2, absent. Outgroup: L1a is strongly expressed in *Lichakephalus* and *Lichakephalina* and weakly expressed in the other lichakephalids.

9. Posterolateral cranidial lobe. In *Acanthopyge (Mephiarges) bifida*, the posterolateral cranidial lobes (the swellings adjacent to the base of the glabella) incorporate prominent spine pairs of the fixigenae during ontogeny (Chatterton 1971: 36). It is thought, therefore, that the posterolateral cranidial lobes belong partly to the glabella and partly to the fixigena (Chatterton 1971: 36). Therefore, it is coded as a separate character because it is thought to be non-homologous with other lateral glabellar lobes. States: 0, absent; 1, present (i.e. *Trochurus*). Outgroup: This swelling is absent in all lichakephalids.
10. L2/bullar lobe/composite lateral lobe. The homology of these lateral glabellar lobes has been much debated (For a review, see Thomas & Holloway 1988, Section 4). They are now thought to be of glabellar origin in all lichids (Thomas & Holloway 1988: 186) and are, therefore, coded as different states within the one character so as not to weight them in the analysis. The bullar lobe (named by Temple 1972) of *Lichakephalus* is thought to be composed solely of L2 (Thomas & Holloway 1988: 189) and it is assumed that the same is true of other lichakephalids. The composite lateral lobe is thought to be derived from fusion of the bullar lobe with other lateral glabellar lobes (cf. *Platylichas* (Thomas & Holloway 1988: fig. 174) with *Amphilichas* (Thomas & Holloway 1988: fig. 246). States: 0, L2 present; 1, bullar lobe present; 2, composite lateral lobe present. Outgroup: Lichakephalids have lobe L2 variously expressed.
11. Definition of L2. These character states are only associated with character 10, state 0 (hereafter designated as character 10:0). States: 0, L2 strongly expressed; 1, L2 weakly expressed. Outgroup: L2 is strongly defined in *Lichakephalus* and *Lichakephalina* and weakly expressed in all other lichakephalids.
12. Width (trans.) of palpebral lobe. States: 0, narrow; 1, wide. Outgroup: Lichakephalids have a narrow (trans.) palpebral lobe.
13. Position of posterior edge of palpebral furrow in relation to glabellar length. States: 0, lying well behind glabellar mid-length; 1, level with glabellar mid-length. Outgroup: The posterior edge of the palpebral furrow of *Acidaspidella* and *Acidaspidina* lies level with the glabellar mid-length. In all other lichakephalids, the posterior part of this furrow lies well behind the glabellar mid-length.
14. Shape of palpebral ridge. States: 0, gently-curving; 1, >-shaped (i.e. in *Arctinurus* and *Oinochoe*). Outgroup: Lichakephalids have a gently-curved palpebral ridge.
15. Size of eyes. States: 0, shorter (exsag.) than 35% of the length (sag.) of the median glabellar lobe; 1, larger than 35% of the length (sag.) of the median glabellar lobe. Outgroup: Where known the lichakephalids have exsagittally small eyes.
16. Tuberculation on preoccipital region. States: 0, distinct nodes absent; 1, distinct nodes present (e.g. *Trochurus*). Outgroup: All lichakephalids have scattered tubercles on the preoccipital glabellar lobe.
17. Occipital structure. States: 0, absent; 1, present as a node, may be weak; 2, as a spine; 3, as a spine pair; 4, medial spine and a pair of lateral spines. Outgroup: Occipital nodes are absent in the lichakephalids.
18. Transverse width of the occipital ring (L0). States: 0, less than palpebral width of cranidium; 1, equal or greater than palpebral width of cranidium. Outgroup: All lichakephalids have a transversely narrow occipital ring.
19. Length of lateral edges of L0 relative to midline length (sag.). States: 0, lateral edges about half sagittal length, or more, of L0; 1, less than half sagittal length. Outgroup: Lateral edges sagittally long in *Lichakephalus* and *Acidaspidina*, sagittally short in all other lichakephalids.
20. Sagittal convexity of cranidium. States: 0, weak; 1, moderate; 2, strong. Outgroup: Lichakephalids show weak convexity.
21. Path of anterior section of facial suture. States: 0, strongly divergent forward; 1, subparallel; 2, convergent forward (there may be subparallel sections within overall convergence). Outgroup: All lichakephalids show the anterior section diverging forward, except *Acidaspidella*, which has a subparallel anterior section.
22. Path of posterior section of facial suture. States: 0, a blunt downwards-directed posterior section (as in *Lichakephalina*); 1, laterally-directed posterior section (as in *Acidaspidella*). Outgroup: *Lichakephalina* has a blunt downwards-directed posterior section, *Acidaspidina* has a longer laterally-directed posterior section. The state for other lichakephalids is unknown.
23. Sub-genal notch. States: 0, indistinct; 1, deep. Outgroup: If the librigenae were not preserved, this state was deduced by the angle of the fixigena. A laterally-directed fixigena implies an advanced genal spine and, hence, a sub-genal notch. Where able to infer, the lichakephalids have no sub-genal notch.

Hypostome

(The hypostomes are not found preserved in the Lichakephalidae)

24. Pitting on middle body of hypostome. States: 0, middle body pitted; 1, middle body not pitted.
25. Hypostome tuberculation. States: 0, hypostome tuberculate; 1, tuberculation on middle body only (e.g. *Dicranopeltis*), may be subdued tubercles on lateral borders (e.g. *Dicranogmus*); 2, tuberculation absent.
26. Shape of anterior lobe of middle body. A subquadrate or trapezoidal middle body results from the position of intersection of the hypostomal middle furrow with the lateral border furrow lying well behind the level of the anterior wings. A rhomboid middle body results in *Dicranopeltis* and *Pseudotupolichas* from the intersection lying opposite the anterior wings (Thomas & Holloway 1988: 194). States: 0, subquadrate/trapezoidal; 1, subrhomboid/rhomboid; 2, subcircular.
27. Maculae. The areas lying laterally in, or on, the posterior side of the middle furrow of the hypostome are termed 'maculae'. They may be flat and indistinct, or elevated and prominent. States: 0, indistinct; 1, prominent.

Thorax

28. Bands of the thoracic pleurae. The thoracic pleurae are not known in many genera but the posterior band of *Acanthopyge*, *Hemiarges* and *Richterarges* is highly inflated relative to the anterior band. States: 0, evenly inflated; 1, posterior band strongly convex, anterior band low. Outgroup: This state is unknown in the lichakephalids.

Pygidium

(All of the following states are unknown for *Acidaspidella*)

29. Development of the pygidial posterior border. States: 0, border furrow absent; 1, border furrow distinct. Outgroup: There is no border furrow present in the lichakephalids.
30. Number of primary pleural spine pairs of pygidium. Secondary marginal spines are ignored. States: 0, none; 1, two; 2, three; 3, four. Outgroup: The pygidial margin is poorly-preserved and so this state is only known for *Lichakephalina* and *Acidaspidina*, both of which have no pleural spines.
31. Shape of pygidial pleural spines in cross-section. These character states are only associated with character 30:1–3. States: 0, dorsoventrally flattened; 1, cylindrical (e.g. *Echinolichas* and *Trochurus*). Outgroup: This character is inapplicable to the lichakephalids, as they have no pleural spines.
32. Presence of posteromedian spine. States: 0, absent; 1, present. Outgroup: This state is only known for *Eoacidaspis*, *Lichakephalina* and *Acidaspidina*, all of which do not have a posteromedian spine.
33. Transverse distance between third pleural spine pair of pygidium. These character states are only associated with character 30:2 and character 32:0. States: 0, wide, equal, or more than half, width of pygidial axis; 1, narrow, less than half width of pygidial axis. Outgroup: This character is inapplicable to the lichakephalids.
34. Development of interpleural furrows. States: 0, very weak or absent; 1, deep. Outgroup: The interpleural furrows of lichakephalids are very shallow.
35. Number of interpleural furrow pairs. States: 0, none; 1, one; 2, two; 3, three. Outgroup: All lichakephalids have no interpleural furrows present.
36. Extent of pleural furrows. States: 0, deep, running to the pleural tip/pygidial border; 1, very weak, effaced; 2, deep, running only to the fulcrum. Outgroup: Pleural furrows of all lichakephalids run close to the pygidial border. The pleural furrows of the pygidia of *Amphilichas*, *Apatolichas* and *Lyralichas* run only to the fulcrum. This expression pattern is also seen in the pleural furrows of the thorax of *Amphilichas* and *Apatolichas*, however these states were not coded here to avoid serial homology codings.
37. Number of pleural furrow pairs. States: 0, two; 1, three; 2, four; 3, five; 4, six; 5, seven. Outgroup: *Lichakephalus* has four pairs of pygidial pleural furrows, *Eoacidaspis* has five or six pairs, *Lichakephalina* has five and *Acidaspidina* seven.
38. Path of third pygidial pleural furrow. These character states are only associated with character 37:1. States: 0, straight; 1, describing a loop posteriorly (e.g. *Conolichas* and *Platylichas (Rontrippia)*). Outgroup: The character is inapplicable to the lichakephalids.
39. Number of complete pygidial inter-ring furrows. States: 0, one; 1, two; 2, three; 3, four; 4, more than four. Outgroup: *Lichakephalus* and *Lichakephalina* have two, *Eoacidaspis* has four and *Acidaspidina* has seven.
40. Number of medially effaced pygidial inter-ring furrows. States: 0, none; 1, one; 2, two; 3, three; 4, more than three. Outgroup: *Lichakephalus* has three, *Lichakephalina* has one and *Acidaspidina* has none.
41. Shape of the bands of the first two pygidial pleurae in cross-section. States: 0, evenly inflated or flattened; 1, posterior band strongly convex, anterior band low. Outgroup: The pleural bands are evenly inflated in all lichakephalids.
42. Condition of the postaxial structure. States: 0, present as a band-like structure (e.g. *Lichakephalus*); 1, absent; 2, modified into a postaxial ridge. Outgroup: The lichakephalids have a postaxial band.
43. Relative width of the postaxial band along anteroposterior axis. These character states are only associated with character 42:0. States: 0, expanding distally; 1, narrowing distally. Outgroup: The axial band of the lichakephalids expands distally.
44. Shape of the terminal axial piece of pygidium. States: 0, tapering evenly back into a postaxial band/ridge; 1, rounded, blunt end; 2, poorly-defined posteriorly. Outgroup: The axial piece of the lichakephalids tapers gently into the postaxial band.
45. General sculpture of pygidium. States: 0, evenly scattered coarse tubercles; 1, fine granules/non-tuberculate. Outgroup: All lichakephalids, except *Lichakephalus*, have non-tuberculate pygidia. *Lichakephalus* possesses evenly scattered tubercles.
46. Depth of furrows delineating pygidial axis. States: 0, deep; 1, shallow. Outgroup: All lichakephalids, except *Eoacidaspis*, have deep furrows.
47. Shape of pygidium in dorsal aspect. States: 0, subsemicircular; 1, subtriangular; 2, subquadrate. Outgroup: All lichakephalids have subsemicircular pygidia.
48. Width of pygidial doublure. States: 0, wide; 1, narrow. Outgroup: All lichakephalids have a wide pygidial doublure.

RESULTS

Maximum-parsimony analysis

The dataset consisted of 48 characters coded for 31 lichid terminal taxa (plus the five lichakephalid outgroup taxa). Ten most parsimonious trees (MPTs) were recovered, with a tree length (TL) of 268 and a consistency index (CI) of 0.4776 (homoplasy index (HI) = 0.6754, retention index (RI) = 0.6056, rescaled consistency index (RC) = 0.2893). The strict consensus tree shows the Lichakephalidae to be monophyletic (Fig. 6). *Lichakephalus* is basal to all other lichakephalids, with *Acidaspidina* and *Acidaspidella* resolving as sister-genera (see clade F; Fig. 7).

The discussion following will summarise the lichid relationships recovered, using the MPT that has the same topology as the majority-rule consensus tree. Character states with ambiguous optimisation are indicated by asterisks

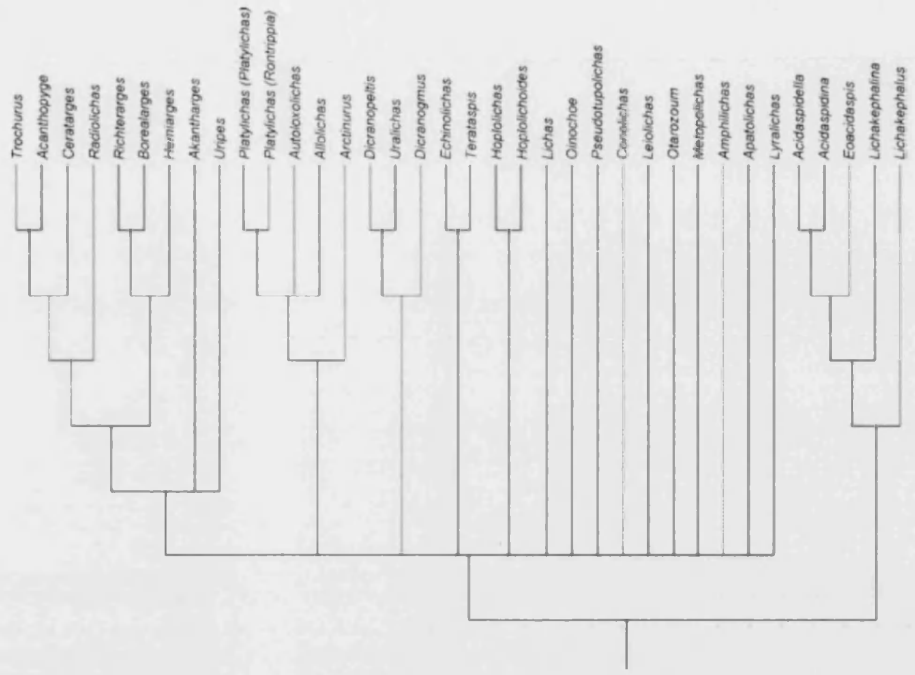

Figure 6 Strict consensus tree recovered from the maximum parsimony analysis.

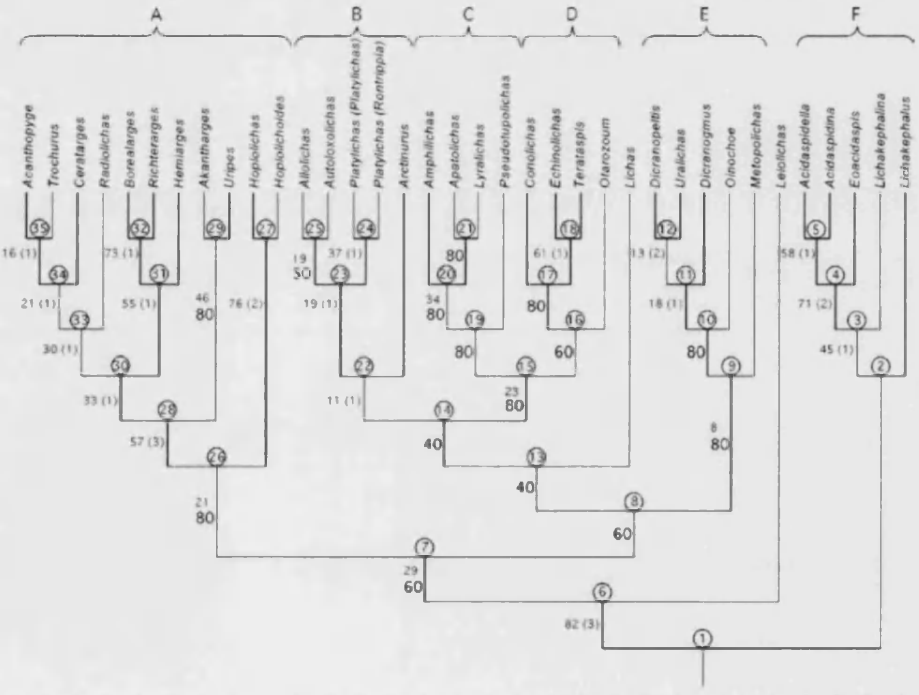

Figure 7 The majority-rule tree (including other compatible groupings) from the maximum parsimony analysis. A low cut-off limit was applied to the bootstrap values figured (bipartitions found in > 50% of trees are shown). Although it is acknowledged that often a bootstrap value of < 50% is considered poor support for a node, it was felt important to convey the difference in support between, for example, the bootstrap support for *Akantharges* and *Uripes* (46%) and that for clades C and D (23%). Bootstrap values and branch support values (given in brackets where > 0) are shown above the branches. The percentage of trees that each group is retained in (where < 100%) is shown below the respective branches in larger font. Branch numbers are displayed within circles and clades A–F are indicated.

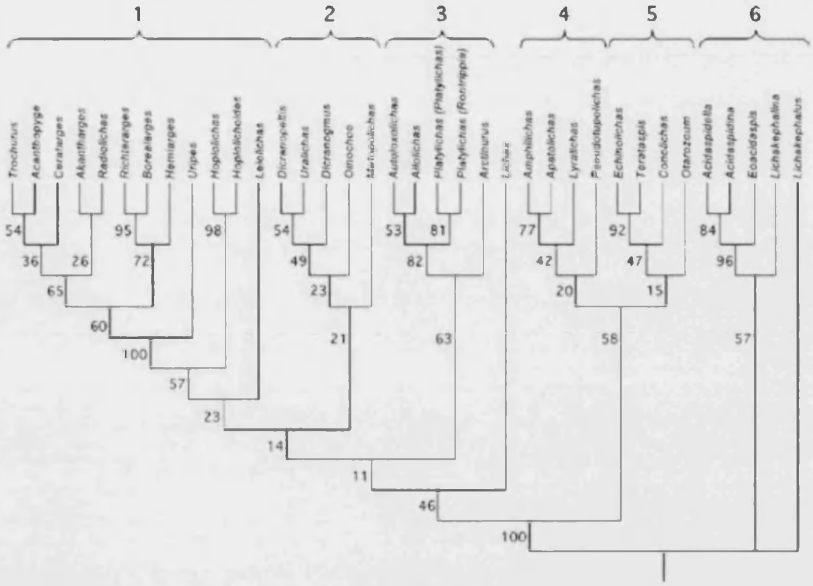

Figure 8 Majority-rule tree (including other compatible groupings) from the Bayesian inference analysis. The percentage of times that a clade occurs among the sampled trees (with the 'burn-in' trees discarded) is displayed above the internal branches. Clades 1–6 are indicated.

within the text, next to the character in question. The Lichidae is monophyletic with respect to the Lichakephalidae. Nine apomorphies robustly support its monophyly (see Systematic Palaeontology, below). Five main clades are seen within the Lichidae: (1) the Trochurinae, *Hoplolichas* and *Hoplolichoides* (clade A), (2) the Platylichinae and *Arctinurus* (clade B), (3) a clade containing the Tetralichinae and *Pseudotupolichas* (clade C), (4) the Echinolichinae, *Conolichas* and *Oinochoe* (clade D) and (5) some Lichinae taxa (clade E: see Fig. 7).

There is support for the Trochurinae Phleger, 1936 (node 28 in clade A: Fig. 7). The Platylichinae receives support, with *Arctinurus* closely-related (node 22 in clade B: Fig. 7). Support is seen for the Tetralichinae Phleger, 1936 (node 20 in clade C: Fig. 7); *Amphilichas* is basal to *Lyralichas* and *Apatolichas*. No support is seen for the Lichinae Hawle & Corda, 1847. However, four out of the seven genera assigned to it (Holloway & Thomas 2002) form a clade (clade E: Fig. 7). The Lichinae, as previously defined, is seen in this analysis as a polyphyletic group; *Arctinurus*, *Pseudotupolichas* and *Lichas* are not included in clade E. *Lichas* resolves basal to clades B, C and D (Fig. 7). Support is seen for the Echinolichinae Phleger, 1936; *Echinolichas* and *Terataspis* being sister groups (node 18 in clade D: Fig. 7). No support is seen for the Homolichinae Phleger, 1936. It is seen here to be a polyphyletic group; *Hoplolichas* and *Hoplolichoides* are basal to the Trochurinae, *Conolichas* and *Otarozoum* are basal to the Echinolichinae, *Leiolichas* is basal to all other lichids (Fig. 7).

Bayesian inference analysis

A tree common to both the MP and BI analysis was searched for, but was not recovered. The BI analysis recognises five main clades within the Lichidae: (1) the Trochurinae, *Hoplolichas*, *Hoplolichoides* and *Leiolichas* (clade 1), (2) some Lichinae taxa (clade 2), (3) a clade containing the Platylichinae and *Arctinurus* (clade 3), (4) the Tetralichinae and *Pseudotupolichas* (clade 4) and (5) the Echinolichinae, *Conolichas*, *Otarozoum* (clade 5: see Fig. 8). The taxon *Lichas* appears basal to clades 1, 2 and 3. The topology of the BI tree differs from that of the majority-rule tree from the MP analysis in: (1) the Platylichinae not forming a clade with those taxa comprising clades 4 and 5 and (2) the Lichinae taxa being closely related to the trochurines.

DISCUSSION

The amount of homoplasy found in the MP analysis presented here (CI = 0.4776) is far lower than that expected from analyses of random data (Klassen *et al.* 1991) and is of similar value for trilobite datasets of similar size (e.g. Ebach & Ahyong 2001 (*Acanthopyge (Lobopyge)*, CI = 0.33); Cotton 2001 (Conocoryphidae, CI = 0.442)). This indicates that the level of homoplasy within the Lichoidea is not unusually high, relative to other derived trilobite groups. However, the absolute degree of homoplasy in the dataset is high. Values of CI for individual character states were assessed and, in the MP analysis, only five have a CI value of 1.0 (characters 10 (0–1, 1–2), 11 (0–1), 13 (0–1) and 28 (0–1)).

This study was exhaustive, but yielded only a few more characters than taxa. This meant that full resolution of lichoid taxa was unlikely to be obtained by cladistic analysis. Some quantitative characters were erected and coded. However, these drastically decreased the resolution of the consensus trees and increased the number of MPTs obtained by MP analysis and, therefore, were omitted from the final analysis.

The consensus trees from both analyses are well resolved, suggesting that they form a good basis for further research. Two of the ten MP trees do not support the close relationship between the taxa of clades C and D;

rather Echinolichinae, *Conolichas* and *Otarozoum* are placed close to the Platylichinae and *Arctinurus*. The MP analysis, therefore, suggests that many characters do not define clades unambiguously and are also in conflict with each other. Characters such as: (1) the proportions of the median glabellar lobe (character 5), (2) the sagittal convexity of the cranidium (character 20), (3) the tuberculation of the hypostome (character 25) and (4) the overall shape of the pygidium (character 48) are particularly homoplastic. Characters that are especially useful in resolving lichoid relationships are: (1) the paths of the cranidial furrows (characters 2 and 3), (2) whether, or not, the median glabella overhangs the anterior border (character 7), (3) the presence, or absence, of the posterocranidial lobe (character 9), (4) the extent of the pleural furrows of the thoracic segments (character 29) and (5) the number of pygidial spines, interpleural furrows and pleural furrows (characters 31, 36 and 38, respectively).

The MP and BI methods produced phylogenetic hypotheses that are largely congruent. Relationships within many of the groups recovered from both analysis types seem stable and robust but the relationships between these groups are dissimilar. The congruence of MP with respect to BI was evaluated by assessing the number of shared nodes and also the congruence between the estimated measures of support (MP bootstrap values versus posterior probability values). However, without knowledge of the true phylogeny it is impossible to tell which tree is more accurate. Twenty-four of the 35 nodes from the MP tree were present in the BI tree. This suggests fair congruence between the tree topologies.

The posterior probabilities of the clades in the BI tree are generally moderately high, except for those branches supporting the Lichinae taxa (Fig. 8). However, it is thought that posterior probability values are systematically higher than non-parametric bootstrap values, as inferred by neighbour joining and maximum likelihood (Leaché & Reader 2002; Cummings *et al.* 2003; Erixon *et al.* 2003; Suzuki *et al.* 2003) and that MP bootstrap scores are not thought be strongly correlated with posterior probabilities (Leaché & Reader 2002). Moreover, it is recognised that bootstrap and posterior probability values are not statistically equal. The former measure is not the MP optimality criteria and the latter is such for BI. However, because the vast majority of cladistic studies rely heavily on MP bootstrap proportions, a reference comparing these and posterior probabilities is considered defensible: Bayesian posterior probabilities provided moderate support (> 60% recovery) for 14 nodes of the phylogeny, whereas the MP analysis provided this level of support for only five nodes (*cf.* Fig. 8 with Fig. 7, respectively).

The support for individual clades recovered from the MP analysis is not particularly high (Fig. 7). Many clades of the majority-rule tree are supported by only a small number of character state changes; such groups are rarely, if ever, recovered during bootstrap resampling (Kitching *et al.* 1998). With analyses conducted at the generic-level, such as these, it is likely that at least one taxon will be revealed that has undergone a simultaneous reversal in nearly all characters that are synapomorphic for the clade. Many bootstrap replicates would sample the numerous reversed characters over the few unambiguous synapomorphies that place the taxon within the group; the bootstrap support for the group would, hence, be disrupted (see Sanderson & Wojciechowski 2000). Indeed, many of the characters used in these analyses were homoplastic in nature. The resulting relationships of the majority-rule tree from the MP analysis are shown in Fig. 9 with the groupings being indicated as previously defined by Thomas & Holloway (1988) and Holloway & Thomas (2002).

It is recognised that this study consists of analyses of only one dataset. Moreover, since the resulting trees from each analysis disagree about the relationships between the deeper branches, it would be impossible to provide a taxonomic system that agrees with the results of both analyses. However, the authors wish to provide a new classification that represents the branching patterns of the main aspects of the analyses.

These analyses suggest a shift in content within some of the existing named groups of lichid trilobites (see Systematic Palaeontology, below). Nearly all of these subfamilial groupings can be expanded to incorporate other closely-related taxa. The classification can, then, only loosely reflect the cladogram from the MP analysis: clades B, C, D, E and *Lichas* are given equivalent taxomonic rank (if the branching pattern of the cladogram was strictly adhered to, then only clades C and D should be given equal taxonomic rank). However, this classification represents the main branching pattern of the MP tree and also incorporates many elements from the BI tree, whilst applying least violence to the existing usage of the taxa.

The two lichoid families Lichida and Lichakephalidae are retained, with the former being comprised of two subfamilies: Trochurinae and Lichinae. It is recognised that the identification of parataxa should be avoided. However, it is desirable to distinguish those monophyletic radiations that arise within clades; especially as, in this case, these radiations relate to previous classifications. The Lichinae as defined here consists, therefore, of four main groups and these are given tribal status: Echinolichini, Tetralichini, Platylichini and Dicranopeltini. However, in recognising these subgroups, those taxa that nest outside the groups of interest (in this case *Leiolichas* and *Lichas*) also merit acknowledgement. The latter taxon, then, is classed as a monogeneric tribe (Lichini). The status of *Leiolichas* is still ambiguous (see Systematic Palaeontology, below).

The relationships resulting from both the MP and BI analyses suggest that the subfamily Trochurini should be expanded to include *Hoplolichas* and *Hoplolichoides*. The relationships are also consistent with the suggestion that *Richterarges* is derived from *Hemiarges* (Thomas & Holloway 1988: 253), but not with the idea that *Acanthopyge* is also derived from *Hemiarges* (Thomas & Holloway 1988: 253). In this analysis, *Acanthopyge* and *Richterarges* are both derived taxa, each positioned robustly within two subclades of the trochurinae (nodes 33 and 31 of Fig. 7, respectively). *Borealarges* has been thought to be closely related to *Richterarges* (Adrain 1994: 1083) and this relationship is supported here (Fig. 7).

The Platylichini can incorporate *Arctinurus* (Figs 7 & 8). The Tetralichinae as defined by Thomas & Holloway (1988) is nested within some basal genera (clades C (Fig. 7) and 4 (Fig. 8)). *Apatolichas* was previously thought to be ancestral to *Amphilichas* and *Lyralichas* (Whittington 1963; Thomas & Holloway 1988). However, both analyses suggest that *Amphilichas* is basal to *Lyralichas* and *Apatolichas*. The Echinolichinae, as defined by Thomas & Holloway (1988), is also nested within a clade. The Echinolichini, then, includes *Conolichas* and *Otarozoum*, which are basal to *Echinolichas*

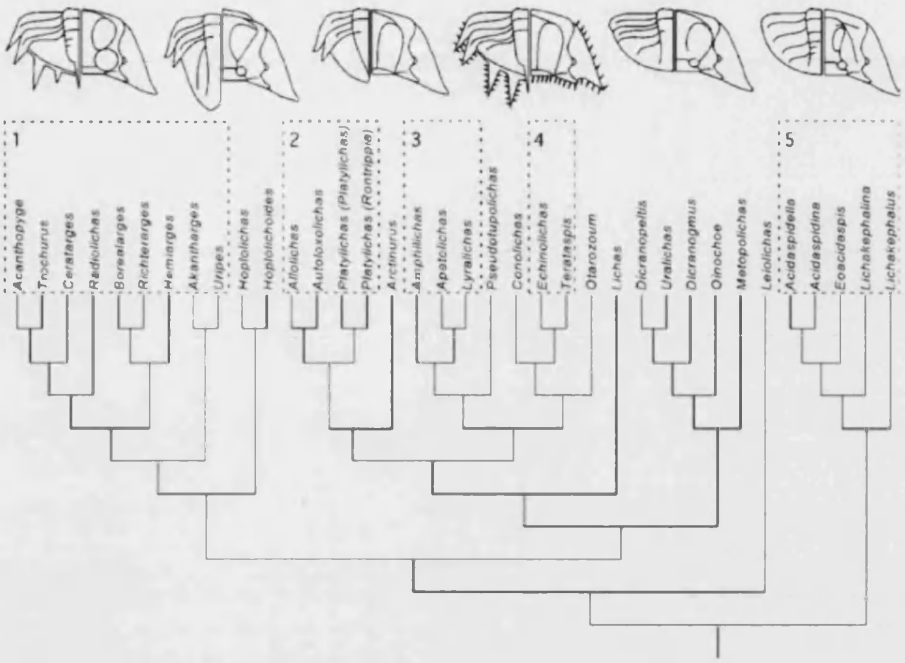

Figure 9 Majority-rule tree (including other compatible groupings) from the maximum parsimony analysis. Schematic illustrations, such as that shown in Fig. 2, of a representative of each group are shown at the top. Taxa as previously defined by Thomas & Holloway (1988) and Holloway & Thomas (2002) are shown in numbered boxes: 1, Trochurinae Phleger, 1936; 2, Platylichinae Phleger, 1936; 3, Tetralichinae Phleger, 1936; 4, Echinolichinae Phleger, 1936; 5, Lichakephalidae Tripp, 1957.

and *Terataspis* in both the MP and BI analyses (see Systematic Palaeontology, below).

Ontogenies are well known for *Acanthopyge*, *Hemiarges* and *Amphilichas*. It would be expected from the phylogenies given here, therefore, that *Acanthopgye* and *Hemiarges* will share more similarities between their ontogenetic stages than either will share with *Amphilichas*. This is, indeed, the case. *Hemiarges* and *Acanthopyge* share: (1) a gently rounded anterior border, (2) three tubercle pairs on the anterior border of late protaspides, (3) the absence of librigenal spines, (4) two large tubercles on the fixigena of early protaspides, (5) no, or one, tubercle on the palpebral lobe of early protaspides and (6) two weak pairs (and sometimes an incipient third pair) of glabellar tubercles (Chatterton 1971, 1980; Tripp & Evitt 1981; Rudkin *et al.* 1994). *Amphilichas*, however, possesses: (1) a concave or straight anterior border, (2) one pair of tubercles on the anterior border of late protaspides, (3) librigenal spines, (4) four large tubercles on the fixigena of late protaspides, (5) two tubercles on the palpebral lobe of late protaspides and (6) four strong pairs of glabellar tubercles (Chatterton 1980; Tripp & Evitt 1981).

SYSTEMATIC PALAEONTOLOGY

Order **LICHIDA** Moore, 1959

Family **LICHIDAE** Hawle & Corda, 1847

[nom. correct. Angelin 1854 *ex* Lichades Hawle & Corda, 1847]

EMENDED DIAGNOSIS. Very narrow preglabellar field (except where spatulate in *Arctinurus* and *P. (Platylichas)* (character 1). Longitudinal furrows that extend to the occipital furrow, if only weakly, and that may also meet with S1 (character 2). Weakly developed S1 furrows that conjoin the longitudinal and axial furrows (except in the Trochurinae and Platylichinae, where they are deeply impressed, and also in most taxa within clades B and C as they do not express S1: character 3). Median glabella does overhang the anterior border (character 7*). Possession of a bullar lobe (the bullar lobes are fused with other lobes to form composite lateral lobes in some taxa within clades B and C: character 10). Moderately convex cranidia (character 20). Subparallel anterior facial sutures (character 21*). Two interpleural furrows (character 35*). One or more complete inter-ring furrow on the pygidial axis (character 39).

TAXA INCLUDED. *Leiolichas* Schmidt, 1885; *Platylichas (Platylichas)* Gürich, 1901; *Platylichas (Rontrippia)* Thomas & Holloway, 1988; *Autoloxolichas* Phleger, 1936; *Allolichas* Krueger, 1992; *Arctinurus* Castelnau, 1843; *Apatolichas* Whittington, 1963; *Lyralichas* Weber, 1948; *Amphilichas* Raymond, 1905; *Pseudotupolichas* Phleger, 1936; *Echinolichas* Gürich, 1901; *Terataspis* Hall, 1863; *Conolichas* Dames 1877; *Otarozoum* Thomas & Holloway, 1988; *Lichas* Dalman, 1827; *Acanthopyge* Hawle & Corda, 1847; *Trochurus* Beyrich, 1845; *Ceratarges* Gürich, 1901; *Radiolichas* Reed, 1923; *Borealarges* Adrain, 1994; *Richterarges* Phleger, 1936; *Hemiarges* Gürich, 1901; *Akantharges* Phleger, 1936; *Uripes* Thomas & Holloway, 1988; *Hoplolichas* Dames, 1877; *Hoplolichoides* Phleger, 1936.

STRATIGRAPHICAL RANGE. Early Ordovician to Middle Devonian.

Genus *LEIOLICHAS* Schmidt, 1885
[*Subfamilia incertae sedis*]

TYPE SPECIES. *Leiolichas illaenoides* Schmidt, 1885.

STRATIGRAPHICAL RANGE. Caradoc.

REMARKS. This genus is monospecific (see Thomas & Holloway 1988: 209). Its phylogenetic position has been uncertain: it was assigned to the Lichinae by Tripp (1957, 1958) and to the Homolichinae by Phleger (1936) and Thomas & Holloway (1988). Here, it falls basal to the Lichidae in the MP analysis. Node 6 is supported by: (1) two pygidial spine pairs (*Leiolichas* has no pygidial spines: character 30), (2) deep interpleural furrows (the interpleural furrows of *Leiolichas* are shallow: character 34) and (3) one medially-effaced pygidial inter-ring furrow (*Leiolichas* has no medially-effaced inter-ring furrows: character 40*). The BI analysis resolves *Leiolichas* as basal to clade 1 (the Trochurinae).

A probable reason for this indeterminacy is that, unlike other lichids, it displays well-developed effacement. Better-preserved specimens that retain more surface sculpture characters (and also the discovery of a hypostome) may place *Leiolichas* in a more derived phylogenetic position, as suggested by the BI analysis. For the moment we leave it as '*subfamilia incertae sedis*'.

Subfamily **LICHINAE** Hawle & Corda, 1847
[*nom. transl.* Gürich 1901 *ex* Lichades Hawle & Corda, 1847]

EMENDED DIAGNOSIS. Median glabella does not overhang the anterior border (reverses in some taxa: character 7*). Hypostome tuberculation absent (tuberculate in *Amphilichas* and *Apatolichas*: character 25).

TAXA INCLUDED. *Platylichas (Platylichas)* Gürich, 1901; *Platylichas (Rontrippia)* Thomas & Holloway, 1988; *Autoloxolichas* Phleger, 1936; *Allolichas* Krueger, 1992; *Arctinurus* Castelnau, 1843; *Apatolichas* Whittington, 1963; *Lyralichas* Weber, 1948; *Amphilichas* Raymond, 1905; *Pseudotupolichas* Phleger, 1936; *Echinolichas* Gürich, 1901; *Terataspis* Hall, 1863; *Conolichas* Dames 1877; *Otarozoum* Thomas & Holloway, 1988; *Lichas* Dalman, 1827.

STRATIGRAPHICAL RANGE. Early Ordovician to Middle Silurian.

Tribe **PLATYLICHINI** Phleger, 1936
[*nom. transl.* Holloway & Thomas 2002 *ex* Platylichinae Phleger, 1936]

EMENDED DIAGNOSIS. Large palpebral lobe (a homoplastic character: character 12). Weakly convex cranidium (character 20). Subquadrate pygidium in dorsal view (character 47).

TAXA INCLUDED. *Platylichas (Platylichas)* Gürich, 1901; *Platylichas (Rontrippia)* Thomas & Holloway, 1988; *Autoloxolichas* Phleger, 1936; *Allolichas* Krueger, 1992; *Arctinurus* Castelnau, 1843.

STRATIGRAPHICAL RANGE. Middle Cambrian to Arenig.

REMARKS. Support for the taxon Platylichinae, as defined by Holloway & Thomas (2002), is seen by: (1) the possession of deeply impressed S1 furrows (seen also in the trochurines: character 3), (2) posteriorly effaced axial furrows (that merge with S1 in *Platylichas*: character 4*) and (3) two medially-effaced inter-ring furrows on the pygidium (only one pair seen in *Autoloxolichas* and *Allolichas*: character 40*).

Tribe **TETRALICHINI** Phleger, 1936
[*nom. transl.* Tripp 1957 *ex* Tetralichadinae Phleger, 1936]

EMENDED DIAGNOSIS. Absence of L1a (character 8). Laterally-directed posteriorly directed posterior section of the facial suture (character 22). Middle body of the hypostome is pitted (character 24).

TAXA INCLUDED. *Apatolichas* Whittington, 1963; *Lyralichas* Weber, 1948; *Amphilichas* Raymond, 1905; *Pseudotupolichas* Phleger, 1936.

STRATIGRAPHICAL RANGE. Arenig/Llanvirn to Ashgill.

REMARKS. The supporting apomorphies for the Tetralichinae as defined by Thomas & Holloway (1988) are: (1) a median glabella that overhangs the anterior border (character 7), (2) tuberculate hypostome (a reversal: character 25*), (3) a narrow distance between the third pygidial pleural spine (character 33), (4) pleural furrows of pygidium run only to the fulcrum (character 36), (5) the presence of two pairs of pleural furrows (also seen in the trochurines and *Lyralichas* has three pairs: character 37) and (6) a narrowing of the postaxial band (character 43). *Apatolichas* and *Lyralichas* both share: (1) one interpleural furrow pair (character 35*), (2) two medially effaced inter-ring furrows (character 40) and (3) a subtriangular pygidium (character 47).

Tribe **ECHINOLICHINI** Phleger, 1936
[*nom. transl.* Balashova *in* Chernysheva 1960 *ex* Echinolichadinae Phleger, 1936]

EMENDED DIAGNOSIS. Hypostome that is tuberculated only on the middle body (known only in *Echinolichas*: character 25*). Prominent maculae (known only in *Echinolichas*: character 27*). Two complete pygidial inter-ring furrows (character 39).

TAXA INCLUDED. *Echinolichas* Gürich, 1901; *Terataspis* Hall, 1863; *Conolichas* Dames, 1877; *Otarozoum* Thomas & Holloway, 1988.

STRATIGRAPHICAL RANGE. Siegenian to Eifelian.

REMARKS. The supporting apomorphies for the *Echinolichas* and *Terataspis* are: (1) L1a is lost (homoplastic character: character 8), (2) a distinct pygidial posterior border (not known in *Terataspis*: character 29*), (3) four pygidial spine pairs (character 30), (4) cylindrical pygidial pleural spines (also seen in the trochurines: character 31), (5) the presence of a posteromedian spine (a homoplastic character: character 32), (6) two medially-effaced pygidial inter-ring furrows (not known in *Echinolichas*: character 40*) and (7) a narrow pygidial doublure (not known in *Terataspis*: character 48*).

Tribe **LICHINI** Phleger, 1936

EMENDED DIAGNOSIS. Small eyes (shorter than 35% of the length of the median glabellar lobe: character 15). Two pairs

of primary pleural spine pairs on the pygidium (character 30).

TAXA INCLUDED. *Lichas* Dalman, 1827.

STRATIGRAPHICAL RANGE. Ashgill to Wenlock.

REMARKS. *Lichas* shares the following characteristics with taxa in clades A, B and C: (1) median glabella does not overhang the anterior border (character 7*) and (2) tuberculation absent on hypostome (character 25).

Tribe **DICRANOPELTINI** Phleger, 1936
[*nom. transl.* Dicranopeltinae Phleger, 1936]

EMENDED DIAGNOSIS. Strongly sagittally convex cranidium (a homoplastic character: character 20).

TAXA INCLUDED. *Dicranopeltis* Hawle & Corda, 1847; *Uralichas* Delgado, 1892; *Dicranogmus* Hawle & Corda, 1847; *Oinochoe* Thomas & Holloway, 1988; *Metopolichas* Gürich, 1901.

STRATIGRAPHICAL RANGE. Llanvirn to Lochkovian.

REMARKS. The phylogenetic position of *Dicranogmus* has proved contentious. The pygidium bears a strong resemblance to that of the lichine *Dicranopeltis* (but the pleural furrow on the third segment is absent) and to that of the tetralichine *Amphilichas*. The latter went extinct during the Ordovician (Adrain 2003) and so perhaps a lichine affinity is more likely. Indeed, this study supports this view: *Dicranogmus* is basal to *Dicranopeltis* and *Uralichas*. The presence or absence of a posterolateral cranidial lobe was coded as ambiguous in *Dicranogmus* as it lacks the prominent cranidial features of the trochurines. If the posterolateral cranidial lobe is coded as present, the topology of the consensus trees is identical to those produced when the character is coded as uncertain (13 MPTs; TL = 226; CI = 0.3673).

The assignment of *Metopolichas* to the Lichinae by Holloway & Thomas (2002) was justified: it is more closely related to taxa previously assigned to the Lichinae than to those previously assigned to the Homolichinae.

Subfamily **TROCHURINAE** Phleger, 1936
[= Argetinae Gürich, 1901; Euarginae Phleger, 1936; Acanthopyginae Erben, 1952; Ceratarginae Tripp, 1957]

EMENDED DIAGNOSIS. Large eyes (reversed in *Richterarges*: character 15). Posterior band of thoracic pleurae highly inflated (unknown in *Hoplolichas* and *Hoplolichoides*: character 28*). Posterior border present on pygidium (character 29). Postaxial structure absent in primitive taxa, modified into a postaxial band in more derived taxa (character 42*). Terminal axial piece of pygidium rounded and blunt ending (poorly-defined in *Hoplolichas* and *Hoplolichoides*: character 44*). Narrow pygidial doublure (character 48).

TAXA INCLUDED. *Acanthopyge* Hawle & Corda, 1847; *Trochurus* Beyrich, 1845; *Ceratarges* Gürich, 1901; *Radiolichas* Reed, 1923; *Borealarges* Adrain, 1994; *Richterarges* Phleger, 1936; *Hemiarges* Gürich, 1901; *Akantharges* Phleger, 1936; *Uripes* Thomas & Holloway, 1988; *Hoplolichas* Dames, 1877; *Hoplolichoides* Phleger, 1936.

STRATIGRAPHICAL RANGE. Llanvirn to Givetian.

REMARKS. The Trochurinae as defined by Thomas & Holloway (1988) is supported by: S1 furrows that conjoin the axial furrow and longitudinal furrow before posterolateral cranidial lobe (character 3). Axial furrows that are expressed on the adaxial side of the posterolateral cranidial lobe (character 4). Median glabella does not overhang the anterior border (character 7*). Absence of glabellar L1a (character 8). Presence of a posterolateral cranidial lobe (character 9). Pygidial pleural spines that are circular in cross-section (character 31).

Family **LICHAKEPHALIDAE** Tripp, 1957
[= Eoacidaspididae Poletaeva, 1957]

EMENDED DIAGNOSIS. Moderately long preglabellar field (character 1). Longitudinal furrow can be effaced but, if not, is not continuous with S0 (character 2). S1 conjoins to S2 to circumscribe the lobe L2, may be effaced (character 3). Median glabella does not overhang the anterior border (character 7). Glabella lobe is L2 (character 10). Sagittal convexity of cranidium is weak (character 20). Path of anterior section of facial suture is strongly divergent (except in *Acidaspidella*, where it is subparallel: character 21). No interpleural furrows are present (character 35). All taxa have more than one complete pygidial inter-ring furrow (character 39).

TAXA INCLUDED. *Lichakephalus* Sdzuy, 1955; *Lichakephalina* Antcygin *in* Varganov *et al.*, 1973; *Eoacidaspis* Poletaeva, 1956; *Acidaspidina* Lazarenko, 1960; *Acidaspidella* Rozova, 1963.

STRATIGRAPHICAL RANGE. Middle Cambrian to Arenig.

REMARKS. See 'Outgroup' (p. 228, above) for comments on the debated monophyly of the lichakephalids. (If *Eoacidaspis* is excluded from the analysis, 45 trees are obtained (TL = 220; CI = 0.3773) and the consensus trees display identical topology to those attained when *Eoacidaspis* is included.) The close relationship between *Acidaspidina* and *Acidaspidella*, within the Lichakephalidae, is supported by: (1) the anterior median glabella being wider, but less than twice as wide, as the posterior (character 5), (2) the posterior edge of the palpebral furrow lying level with the glabella mid-length (character 13), (3) seven pygidial pleural furrows (character 37*) and (4) having more than four complete pygidial inter-ring furrows (character 39*).

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APPENDIX: CHARACTER DATASET FOR THE LICHOIDEA

See the main text for explanation. A question mark (?) indicates missing data. Where characters are polymorphic, the alternative states are listed beneath.

Taxa	10	20	30	40	
Lichakephalus	1000000000	0?0??00000	0?0?????0?	???0002?13	000000??
Acidaspidella	1400100100	1?1??00010	110???????	??????????	????????
Eoacidaspis	1400020100	1000000010	0?0?????0?	?0?0003?3? 4	0000110?
Lichakephalina	1002000000	0?0??00010	00?????00	?0?0003?11	00001000
Acidaspidina	14?0120100	1?1?000000	010?????00	?0?0005?40	00001000
Lichas	0110000001 2	??0?000001	1001200?01	00?1201001	00000000
Arctinurus	2210000001	?101100100	1101200002	0001201001	00000020
Dicranopeltis	0020000001 11	?10?100012	1010110?02	0011201001	00100010
Oinochoe	0110001001 1	?101000002	2101101?03	00?12010??	00000000
Pseudotupolichas	0350100202	?000000101	1100210?02	0001201001	00000020
Uralichas	0020001001 2	?000000011	2?0100??01 2 3	01???00?01 1 12 2 3	02?00010
Echinolichas	0350101202	?100100001	2001101?13	11?12010??	00100001
Terataspis	?35??01202	?0????0002	??1????0?3	11?120???2	0000000?
Autoloxolichas	0021000001	?100101000	1001201?02	00?0210?02	0010?1?0
Conolichas	0350101002	?000100012	200?????02	0001201110	00000000
Hoplolichas	0110101001	?000?04001	110?????12	00?1200?01 1	01?20001
Hoplolichoides	?110100001	?000103001	110?????12	00?1200?01 1	01?20021
Leiolichas	0110021001	??0??00001	????????00	?0?0310?00	0010110?
Otarozoum	0350000002	?000100001	100????002	0001201011	00100000
Platylichas (Platylichas)	2122020001	?100100000	2001200002	0001201002	0000102?
Platylichas (Rontrippia)	0122000001	?????00000	2000200?02	0011201102	000?001?
Metopolichas	0110100001 2 1	?000000002	1000100?02	0001201001	00000?2?
Amphilichas	0350001202	??0??00001	11?0000?02	0011220?01	00100000
Apatolichas	0351001102	?100101001	??00000002	0010120?02	01??001?
Lyralichas	0450001202	?000?00001	??012?0?03	00?1322?12	0010001?
Trochurus	0133201011 24	?0???10012	2011100?12	1001200?01	12?00001
Acanthopyge	0133100211 1	?0???00002 4	2011100112 1 3	10?1200?01 1	12?00001
Akantharges	0133000211	?0???00002	200?1???02 1	1000?1??04	01?11001
Ceratarges	0133231211	?0???01002	201????112	11?1?0??0?	12?11001
Hemiarges	0133000111 24 1	?000?00001	100??01113	10?1200?11	12?10021
Radiolichas	0133200221	?00?110001	2011201?02	11?1?0??00	02?100??
Richterarges	0033100211 114	?000000011	100?10?113 21	10?1200?33 1	12?10001
Uripes	0133000111 12 1	?000100001	1001200110 2	?0?0210?01	0001002?
Borealarges	0133110211 1 1	?000?00011 1	1000101?13	11?1200?12	12?10001
Allolichas	0121000001	?100101000 2	100????012	00?1201011 2	000??0??
Dircranogmus	01??0010?1	?000000002	2001100002	0011200?01	00100010

Chapter 3: Phylogeny of the suborder Calymenina

3. The phylogeny of the suborder Calymenina (Trilobita)

3.1 TAXONOMIC HISTORY OF THE CALYMENOIDEA

'Another calymenid!...Shirley you jest!' - with kind acknowledgements to Dr. Edgecombe (Australian Museum, Sydney)

THE order Phacopida Salter, 1864 is the largest group outside the Libristoma and currently consists of the suborders Calymenina Swinnerton, 1915, Cheirurina Harrington & Leanza, 1957 and Phacopina Struve *in* Moore, 1959. The relationships between these three suborders are contested; some consider the calymenines to be unrelated to the latter two groups. Eldredge (1977) placed them as sister group to 'some Ptychopariina' whilst others considered the suborders to comprise a monophyletic group that falls outside the Libristoma (e.g. Fortey 1990).

The genus *Calymene* Brongniart 1822, which gives the group its name, was founded as early as 1822 (Brongniart) and the family Calymenidae was erected in 1840 (Milne-Edwards). The family was formally revised by Schmidt (1894) and Pompeckj (1898): the latter author recognized several groups of species within a restricted *Calymene*.

Shirley (1936) produced a seminal and comprehensive overview of all calymenid genera then recognized. He divided the genera into two groups: Group A, that consisted of taxa without papillate glabellar lobes or buttresses on the fixigena, and Group B, that consisted of those taxa with papillate glabellar lobes and corresponding buttresses (Shirley 1936, p. 394-5; see Plate 3 (g) for examples). This division has remained useful and is still adopted (e.g. Whittington 1971b).

The Calymeninae has been well studied from many angles (e.g. Chatterton *et al.* 1990; Hammann 1977, 1983, 1985; Hammann & Leone 1997; Henry 1980; Siveter 1977, 1979, 1980, 1983, 1985, 1996; Whittington 1971b) but very few groups (i.e.

subfamily Reedocalymeninae Hupé, 1955 (see Turvey 2002b) and genus *Alcymene* Ramsköld *et al.* 1994) have been subjected to rigorous cladistic methods.

The status of *Colpocoryphe* Novák *in* Perner, 1918 and *Salterocoryphe* Hammann, 1977 is contentious. They have been placed within both the Calymenidae (e.g. Hupé 1955; Henry 1970, 1980; Hammann 1983) and Homalonotidae (e.g. Sdzuy 1957, 1959; Bergström 1973; Thomas 1977). Both *Neseuretus* Hicks, 1873 (Sdzuy 1957; Whittard 1960; Thomas 1977) and *Plaesiacomia* Hawle & Corda, 1847 (Hughes 1969; Thomas 1977) have also been the subject of the same confusion. In addition, some workers consider them to constitute the Colpocoryphinae Hupé 1955, whereas other workers consider them to occupy different subfamilies (e.g. Henry (1980) considered *Colpocoryphe* to be within the Colpocoryphinae Hupé, 1955 and *Salterocoryphe* within the Flexicalymeninae Siveter, 1977).

The Homalonotidae are typically known from old, inadequate descriptions. However, there has been valuable recent work on some taxa (e.g. Tomczykowa 1975; Thomas 1977; Wenndorf 1990; Whittington 1993). A phylogeny of the whole suborder is long overdue.

3.2 DISTRIBUTION OF THE CALYMENOIDEA

Early forms are *Pharostomina* from the Tremadoc of Argentina and Germany, *Bavarilla* and the bathycheilines. Two stocks are seen in the southern province (South America-Mediterranean-Asia-Australia region) from *Neseuretus* and *Pharostoma* (Whittington 1966). *Neseuretus* appears in the earliest Arenig in Britain and other calymenids are found in southern Europe a little later. In southeast Asia there was a considerable radiation and the genera *Reedocalymene* and *Calymenesun* appear.

In the Llanvirn and Caradoc, *Flexicalymene* and *Diacalymene* are seen in Britain and *Vietnamia* and *Reedocalymene* in S. E. Asia. Some genera are seen later in the northern province (North America and Balto-Scandia-Russia region), e.g. *Pharostoma* in the Llandeilo and *Flexicalymene* in the Caradoc of North America, with more genera reaching North America by the Ashgill (Hammann 1983).

Platycoryphe and *Colpocoryphe* appear in Britain in the Llanvirn-Llandeilo (Whittard 1955-1967), as did *Calymenella* in the Mediterranean: *Brongniartella* appearing in the Caradoc. Migrants into the northern region in the Caradoc and Ashgill are *Platycoryphe* and *Brongniartella* (Whittington 1966): the latter being widespread in

northern Europe too. Homalonotines persist into the Middle Devonian (e.g. *Dipleura*) although they are rare in the Ashgill and even more so in the Llandovery (Thomas 1977).

3.3 PHYLOGENETIC ANALYSIS

3.3.1 TAXONOMIC SAMPLING

Given the broad scope of this study, character state assignments were determined primarily on the basis of published descriptions and illustrations. However, much unpublished literature and fossil material from the library and collections of DJS were used. In general, type species were coded. However if these were poorly known, better-preserved species (which could be established as congeneric) were coded instead (asterisks indicate these taxa in Table 3.1). All taxa included in the analysis are listed in Table 3.1 below.

Onnicalymene Dean, 1962, *Reacalymene* Shirley, 1936 and *Apocalymene* Chatterton & Campbell, 1980 were coded, as their taxonomic level is contentious (see Siveter 1977, p. 357 and p. 375 for discussion of the status of *Onnicalymene* and *Reacalymene*; Holloway 1980 and Sandford 2000 for discussion of *Apocalymene*). *Liocalymene* Raymond 1916 is poorly-known and its phylogenetic position is uncertain; it is known only from two species (*Liocalymene clintonii* and *L. cresapensis*) and both of these were coded.

Limbocalymene Maximova, 1978, *Paracalymene* Pillet, 1968, *Ptychometopus* Schmidt, 1894, *Scabrella* Wenndorf, 1990 and *Burmeisteria* Salter, 1865 were excluded as they were either badly documented or tentatively assigned to the Calymenina. *Leiostegina* Kobayashi, 1937 was excluded from the analysis; the type material of the only known species is lost and illustrations are poor (see Thomas 1977, p. 160).

Family Calymenidae MILNE-EDWARDS 1840			
	Subfamily Calymeninae MILNE-EDWARDS 1840		
		Calymene	BRONGNIART 1822
		*Diacalymene**	KEGEL 1927
		Dekalymene	CURTIS & LANE 1998
		Tapinocalymene	SIVETER 1980
		Arcticalymene	ADRAIN & EDGECOMBE 1997
		Alcymene	RAMSKÖLD *ET AL.* 1994
		Papillicalymene	SHIRLEY 1936
		Spathacalymene	TILLMAN 1960
		Nipponocalymene	KANEKO 1985
	Subfamily Flexicalymeninae SIVETER 1976		
		*Gravicalymene**	SHIRLEY 1936
		Metacalymene	KEGEL 1927
		Sthenarocalymene	SIVETER 1977
		Platycalymene	SHIRLEY 1936
		Flexicalymene	SHIRLEY 1936
		*Flexicalymene (Flexicalymene)**	SHIRLEY 1936
		*Flexicalymene (Onnicalymene)**	SHIRLEY 1936
		Flexicalymene (Reacalymene)	SHIRLEY 1936
		Thelecalymene	WHITTINGTON 1971a
		Linguocalymene	TOMCZYKOWA 1991
		Apocalymene	CHATTERTON & CAMPBELL 1980
		?Liocalymene	RAYMOND 1916
	Subfamily Reedocalymeninae HUPÉ 1955		
		?Calymenella	BERGERON 1890
		Calymenesun	KOBAYASHI 1951
		Neseuretinus	DEAN 1967
		*Neseuretus [Synhomalonotus]**	HICKS 1873
		?Pharostomina	SDZUY 1955
		Pradoella	HAMMANN 1977
		*Reedocalymene**	KOBAYASHI 1951

		Sarrabesia	HAMMANN & LEONE 1997
		Vietnamia	KOBAYASHI 1960
		?Protocalymene	ROSS 1967
	?Subfamily Colpocoryphinae HUPE 1955		
		*Colpocoryphe**	NOVÁK *IN* PERNER 1918
		Salterocoryphe	HAMMANN 1977
Family Homalonotidae CHAPMAN 1890			
	Subfamily Homalonotinae CHAPMAN 1890		
		Homalonotus	KÖNIG 1825
		Brongniartella	SALTER 1865
		Burmeisteria	SALTER 1865
		*Burmeisterella**	REED 1918
		Digonus	GÜRICH 1909
		*Dipleura**	GREEN 1832
		*Parahomalonotus**	REED 1918
		Trimerus	GREEN 1832
		Arduennella	WENNDORF 1990
	Subfamily Kerfornellinae HENRY 1980		
		Kerfornella	HENRY 1976
		Plaesiacomia	HAWLE & CORDA 1847
	Subfamily Eohomalonotinae HUPÉ 1953		
		Iberocoryphe	HAMMANN 1977
		*Eohomalonotus**	REED 1918
		*Huemacaspis**	PŘIBYL & VANĚK 1980
		*Platycoryphe**	FOERSTE 1919
	Subfamily Bavarillinae SDZUY 1957		
		Bavarilla	SDZUY 1957
Family Bathycheilidae PŘIBYL 1953			
	Subfamily Bathycheilinae PŘIBYL 1953		
		Calymenia	KOLOBOVA *in* SOKOLOV& ĚLKIN 1978
		*Bathycheilus**	HOLUB 1908
		*Parabathycheilus**	MERGL 1984

		Eulomina	RŮŽIČKA 1931
	Subfamily Pharostomatinae HUPÉ 1953		
		Pharostoma [*Prionocheilus*]	HAWLE & CORDA 1847
		Thulincola	TRIPP 1962
		Holoubkocheilus	MERGL 1994

Table 3.1: Authorship references for taxa included in the cladistic analysis. Type species of genera regarded as junior synonyms are indicated by the name of the synonymous genus in square brackets. Question marks precede taxa that are especially tentatively taxonomically-placed prior to this analysis. An asterisk indicates taxa where the type species was not coded. The scheme of Hammann (1983) is loosely followed.

3.3.2 METHODS

The dataset was tested for significant non-random structure using the permutation tail probability (PTP) test (1000 replicates with heuristic search via 100 random stepwise additions and TBR branch-swapping) (Faith & Cranston 1991). The most parsimonious tree (MPT) for the original dataset is calculated. The states of each character are then permuted among the taxa, whilst maintaining the proportions of each state, to produce a new dataset. This new dataset is then analysed and the length of its MPT is calculated. This permutation is repeated (1000 times in this study) and the PTP is defined as the proportion of all datasets that yield cladograms equal to or shorter than those produced from the original dataset The null hypothesis of no cladistic structure can be rejected if the *p*-value is less than, or equal to, 0.05 (i.e. no more than 5% of the sets of MPTs from the randomized data sets were as short as or shorter than the MPT(s) from the original dataset; Kitching *et al.* 1998). The PTP test ($P<0.01$) indicated that there was significant non-random structure in the dataset; further analyses could then be conducted confidently.

The dataset from Appendix I was analyzed using PAUP (version 4.0b10*, Swofford 2002). All characters were equally weighted, but characters 19 (adaxial structure of S1: no immediate lobe - barely perceptible lobe – defined lobe present) and 39 (preglabellar area: roll-like – short with subtransverse ridge present – long and gently sloping) were treated as additive (ordered) as their states are thought to represent clear transformation series. A heuristic search was employed (via 100 random stepwise additions and TBR branch-swapping). Character states were reconstructed using the

'accelerated transformation optimisation' criterion (ACCTRAN). Some of the species exhibit different character states for certain characters and some characters had to be coded as uncertainties; hence, multistate taxa were coded as 'variable with respect to the bracket type'.

Bootstrap proportions (10,000 replicates with starting tree(s) obtained via *fast* stepwise addition with random addition sequence, branch-swapping algorithm: none; Felsenstein 1985) were calculated to measure the frequency of a branch's occurrence in the resampling of pseudoreplicates from the dataset (and, thus, its strength of support). Ideally, bootstrap searches should be calculated by a heuristic search (via random stepwise additions and TBR branch-swapping) as this is would be a more comprehensive exploration. However, this method was not computationally feasible with this dataset because the computer quickly ran out of memory (2.1 GHz PowerPC G5 processor). The fast stepwise-addition analysis is expected to provide bootstrap support estimates of support that are less than those obtained when a more comprehensive method is used.

The trade-off between speed and accuracy was deemed reasonable, as the obtained figures are more likely to be an underestimation rather than an overestimation: both simulation studies and those on real datasets suggest as much (see DeBry & Olmstead 2000 and Mort *et al.* 2000 respectively).

Branch support indices (Bremer 1988, 1994) were calculated in TreeRot (Sorenson 1999). These values provide a measure of relative support for each clade, i.e. the number of additional steps that are required before a clade is lost from the strict consensus tree of the minimum-length cladograms (Kitching *et al.* 1998). TreeRot aids in the determination of these indices by generating a command file that can be run through the computer program PAUP* (Swofford 2002). The command file includes: (1) a constraint statement for each node in a given shortest tree; and (2) commands to search for trees inconsistent with each of these constraint statements in turn. Compared to the shortest tree, the number of additional steps required in the shortest tree that is *inconsistent* with a given node is the Bremer support index for that particular node. For nodes with decay indices of more than 3, the constraint statement approach is much more effective than simply finding all trees 1, 2, 3, etc. steps longer than the shortest tree and then examining their strict consensus for which nodes are lost. The ensemble consistency index (CI) (Kluge and Farris 1969) in PAUP was used to examine the relationship between the entire dataset and a particular tree topology and, hence,

measures the level of homoplasy in the dataset. The ensemble retention index (RI) (Farris 1989) measures support for the trees based on the similarity due to synapomorphy only. Uninformative characters were excluded from the analyses as these can affect both the CI and RI in a parsimony analysis (Smith 1994). The morphological dataset was entered into MacClade Version 4.06 (Maddison & Maddison 2003) to investigate patterns of character evolution.

3.3.2.1 *Outgroup. Bavarilla hofensis* (Barrande 1868) is used as the outgroup; it appears stratigraphically early (Sdzuy 1955, 1957; Whittington 1965; Thomas 1977) and is commonly thought to be a basal calymenid (Hammann 1983; Fortey 2001; Turvey 2002b).

3.3.2.2 *Characters.* Some calymenoid ontogenies are known: *Calymene sp.* Brongniart, 1822 (Chatterton *et al.* 1990, p. 270-271); *Flexicalymene senaria* (Conrad 1841) (Chatterton *et al.* 1990, p. 266-270); *Brongniartella sp.* Reed, 1918 (Chatterton *et al.* 1990, p. 271-275); and *Apocalymene coppinsensis* Chatterton & Campbell, 1980 (Chatterton & Campbell 1980, p. 93-97). Characters of small growth stages were coded into the dataset using the character list from Chatterton *et al.* 1990 (p. 271). However, only one character was informative at this relatively low-level analysis (Chatterton *et al.*'s character 18). The terminology adopted here is identical to that used in the *Treatise*, unless otherwise stated. The character number in the following list corresponds directly to its number in the dataset (Appendix I).

Whole exoskeletal characters

1. Ratio of entire exoskeletal shape (exclusive of anterior process):
    0. Length/ Width = 1.7 or greater
    1. Length/ Width = 1.7 or less

2. Cephalic length (sag.) greater or less than one third post-cephalic length:
    0. Greater than
    1. Equal to, or less than

3. Cephalic length (sag.) vs. pygidial length (sag.):

0. Pygidial length markedly shorter than cephalic length
1. Pygidial length subequal to (90-110% times) cephalic length
2. Pygidial length easily exceeding cephalic length

4. Sculpture:
0. Variously tuberculate
1. Evenly granulate
2. Granulate, with enlarged tubercles on anterior adaxial part of fixed cheek, e.g. *Tapinocalymene*
3. Relatively smooth
4. Evenly granulate with various spines evenly displayed along the body, e.g. *Burmeisterella*

Cranidium

5. Facial sutures:
0. Opisthoparian
1. Gonatoparian
2. Proparian

6. Anterior branch of facial sutures (from γ to α):
0. Subparallel
1. Convergent
2. Convergent, anterior sections join each other axially to form a triangular shape of the frontal area of the cranidium, e.g. *Trimerus delphinocephalus*

7. Postocular suture (posterior branch of facial suture):
0. Straight
1. Sigmoidal, posteriorly directed without outwards turn
2. Sigmoidal, posteriorly directed with outwards turn, e.g. *Calymene*

8. Relative posterior fixigenal width:
0. Equal/or less than that of glabella at occipital ring
1. Greater than that of glabella at occipital ring

9. Glabellar shape:
    0. Parabolic/trapezoidal, e.g. *Neseuretus*, *Flexicalymene*
    1. Convex outwards basally, tapering anteriorly (bell-shaped), e.g. *Calymene*
    2. Little tapering, subrectangular, e.g. *Calymenella*
    3. Concave inwards basally with severe tapering anteriorly, e.g. *Eohomalonotus brongniarti*

10. Anterior margin of glabella:
    0. Transverse
    1. Uniformly rounded
    2. Weakly medially concave, e.g. *Neseuretinus*

11. Number of glabellar furrows:
    0. 4
    1. 3
    2. 2, S3 indistinct
    3. all absent or very weak, e.g. *Plaesiacomia*
    4. S1 distinct, all others absent or weak, e.g. *Eohomalomotus*
    5. S1 and S2 distinct, others absent, i.e. *Platycorphe dyaulax*

12. 1S:
    0. Not shallowing abaxially
    1. Shallowing abaxially

13. Length of L1 (sag.):
    0. Equal to, or less than, L2 and L3 together
    1. Greater than L2 plus L3

14. Furrow defining L1 (or posterior branch of S1):
    0. Straight
    1. Curved
    2. Sigmoidal, i.e. *Calymenella*

15. Separation of L1 from median lobe by furrow:
    0. Not separated
    1. Separated, even if only by a shallow depression
16. Separation of L2 from median lobe by furrow:
    0. Not separated
    1. Separated, even if only be a shallow depression

17. Shape of L2:
    0. Subcircular
    1. Transversely elongate

18. S1:
    0. Forked
    1. Unforked

19. Adaxial structure of S1:
    0. Forked adaxially, but not forming intermediate lobe, e.g. *Alcymene*, *Diacalymene drummuckensis*
    1. Barely perceptible intermediate lobe between bifurcating S1, e.g. *Reacalymene*
    2. Forked adaxially, forming intermediate lobe between bifurcating S1, e.g. *Arcticalymene*, *Calymene*

20. L2 with or without buttress (papillae and buttresses are only coded as present if they are seen as paired structures with contact at their extremities):
    0. Without
    1. With, e.g. *Calymene*, *Alcymene*

21. L3 with or without buttress (papillae and buttresses are only coded as present if they are seen as paired structures with contact at their extremities):
    0. Without
    1. With, i.e. *Arcticalymene*, *Papillicalymene*

22. Convexity of L3:
    0. Independent of glabella
    1. Not independent of glabella

23. Length of occipital ring (sag.):
    0. Subequal
    1. Medially longer

24. Occipital tubercle:
    0. Absent
    1. Present
    2. Present as a small spine, e.g. *Burmeisterella armata*
    3. Present as a long spine, e.g. *Arduennella maillieuxi*

25. Occipital muscle pad:
    0. Not impressed
    1. Impressed, e.g. *Neseuretinus*

26. Paraglabellar areas (arcuate, slightly depressed area at inner, posterior corner of fixigena, near S1; coding only those that are flattened and dorsalised):
    0. Absent, e.g. *Liocalymene*
    1. Present – faint, e.g. *Calymenella*
    2. Present – distinct, e.g. *Pradoella*
    3. Contained in axial furrows, e.g. *Calymenia*

27. Palpebral lobe position (exsag.):
    0. Mid-length (exsag.) opposite anterior part of 1L/1S
    1. Mid-length opposite 2L
    2. Mid-length opposite 2S/3L
    3. Mid-length opposite 3S

28. Palpebral lobe position (trans.): ratio of width of preocular fixed cheek to that of glabella at L2:
    0. Up to 0.4

1. Over 0.4

29. Palpebral lobe length (exsag.) relative to length (sag.) of occipital ring:
    0. Less than (<85%)
    1. About equal (85-115%)
    2. More than (>115%)

30. Eye ridge:
    0. Present
    1. Absent

31. Fossulae (depression near anterolateral edge of glabella):
    0. Present
    1. Absent

32. Anterior nodes (paired nodes that lie within the fossulae, close to the anterolateral corner):
    0. Absent
    1. Present, e.g. in *Reedocalymene expansa* and *Calymenesun tingi*

33. Posterior border furrow:
    0. Constantly short (exsag.) (ptychoparyoid style), e.g. *Platycalymene*
    1. Lens like, e.g. *Metacalymene*

34. Posterior border of fixigena:
    0. Straight, e.g. *Calymene*
    1. Distinct anteriorly-directed 'curling-up', e.g. *Eohomalonotus*

35. Articulation notch on posterior cephalic margin:
    0. Marked by more weak, rounded deflection of margin, e.g. *Neseuretus*
    1. Marked by distinct angular deflection of margin, e.g. *Apocalymene*
    2. Absent, e.g. *Pradoella*

36. Distance of articulating point, if present, from axial furrow relative to width of occipital ring:

0. Less than half transverse width of occipital ring
1. More than half transverse width of occipital ring

37. Preocular fixigena appearance:

0. Anterior adaxial margin rounded, and not greatly overhanging the anterior border furrow, e.g. *Platycalymene*
1. Anterior adaxial margin pointed, overhanging anterior border furrow, e.g. *Alcymene alveus*
2. Not or weakly defined by anterior border furrow (*Diagonal-Furche* of Hammann 1983), e.g. *Calymenella*

38. Preglabellar field:

0. Absent
1. Present

39. Preglabellar area:

0. Short (sag.) and roll-like, e.g. *Calymene*
1. Subtransverse ridge present, a noticeable break in the slope present, e.g. *Diacalymene*
2. Gently sloping, very long with no break in slope (note: longer than the preglabellar area of *Calymene puellaris*, which is very variable), e.g. *Linguocalymene*

40. Preglabellar field (if character 38:1):

0. Not inflated
1. Inflated, e.g. *Neseuretus*

41. Fixigenal spine:

0. Absent
1. Present

42. Anterior border of cranidium:

0. Fairly straight or gently curved
1. Broad, dorso-ventrally flattened 'point' e.g. *Calymenella*
2. Distinct thin spine, e.g. *Reedocalymene*, *Calymenesun*
3. Tongue-like process, can be inflected towards glabella, e.g. *Spathacalymene* and *Linguocalymene*
4. Straight, with a small prominence that is the rostral prominence

43. Anterior border length (i.e. that part of preglabellar area underlain by doublure) *cf.* length (sag.) of occipital ring:

0. Less than
1. About equal to
2. More than

44. Inner anterior corner of fixigena:

0. Not pointed
1. Pointed, e.g. *Spathacalymene*
2. 4p defined, e.g. *Papillicalymene*

45. Preglabellar furrow:

0. Present, deep
1. Present, shallow/ not impressed
2. Shallow and broad

46. Glabella:

0. Low, fails to protrude anteriorly beyond the fixigenae, e.g. *Metacalymene*
1. More raised, forwardly-protruding glabella, e.g. *Apocalymene*

47. Occipital furrow:

0. Strongly imprinted right across, narrow
1. Shallow adaxially, may be broad (sag.), e.g. *Eohomalonotus*

Librigenae

48. Lateral border furrow:

0. Very shallow
1. Moderately deep
2. Deep
3. Absent

49. Eye socle (i.e. the platform on the upper part of the librigenae that lies below the visual surface of the eye (Siveter 1980), defined by an 'eye socle furrow'):

0. Present
1. Absent

50. Librigenal spine:

0. Absent
1. Present

51. Marginal spines on lateral border:

0. Absent
2. Present, e.g. *Pharostoma pulchrum*

Rostral plate and hypostome

52. Hypostoma:

0. Anterior border long (sag.) and flange like, e.g. *Platycalymene*
1. Anterior border short

53. Hypostomal rhynchos:

0. Absent
1. Present, e.g. *Alcymene*
2. Present and doubled, e.g. *Nippocalymene*

54. Maculae:

0. Prominent
1. Subdued

Thorax

55. Number of thoracic segments:
    0. 13 segments
    1. 12 segments

56. Lateral lobes on axial rings:
    0. Undeveloped, e.g. *Alcymene*
    1. Developed, e.g. *Reacalymene*, *Calymene*

Pygidium

57. Pygidial border defined by furrow (may be poorly-defined), known as a 'pseudoborder' (Fortey 1990):
    0. Border present
    1. Border absent

58. Pygidium:
    0. Two-thirds or less as long as wide
    1. Two-thirds or more as long as wide

59. Number of pygidial axial ring furrows:
    0. 4 or less
    1. 5 to 9
    2. 10 or more

60. Vincular region:
    0. Absent, e.g. *Dipleura*
    1. Present, defined by a break in the height and sculpture of the pleurae, e.g. *Calymene*
    2. Present, defined clearly by a vincular furrow (the 'cinctures' of Dean and Zhou 1988), e.g. *Colpocoryphe*

61. Postaxial ridge:

0. Absent
1. Present

62. Pygidial furrows:
    0. Interpleural furrows present only abaxially, accompanied by flared pleural furrows, e.g. *Arcticalymene*
    1. Complete interpleural furrows present (may be weak), complete pleural furrows present, e.g. *Calymenella*, *Platycalymene*
    2. Complete interpleural furrows present, incomplete pleural furrows present, e.g. *Protocalymene*
    3. Interpleural furrows present only abaxially, normal pleural furrows present, e.g. *Neseuretinus*
    4. No interpleural furrows and normal pleural furrows present, e.g. *Iberocoryphe*
    5. Both interpleural and pleural furrows absent; pygidial pleurae smooth, may have deeply incised first pleural furrow, e.g. *Huemacaspis*

63. Axial vs. pygidial width:
    0. Axis greater than one-third pygidial width
    1. Axis less than one-third pygidial width

64. Pygidial trilobation:
    0. Distinct
    1. Distinct, but shallow
    2. Obsolete/ indistinct

65. Convexity of pygidial axis:
    0. High
    1. Low

Ontogeny

66. Presence of three large marginal spines (anterior fixigenal spine, midfixigenal spine and posterior fixigenal spine) on the protocranidium:

0. Absent
1. Present

3.3.3 RESULTS

The resulting dataset consists of sixty-six characters using fifty-five calymenoid genera. Two most parsimonious trees (MPTs; Figure 3.1) were recovered, with a tree length (TL) of 426 and a CI of 0.25 (homoplasy index (HI) 0.75, RI 0.63, rescaled consistency index (RC) 0.16). The majority-rule tree shows the following: (1) the Calymenidae Milne-Edwards, 1840 is paraphyletic with respect to the Bathycheilidae Přibyl, 1953; (2) the Reedocalymeninae Hupé, 1955 is basal to the Flexicalymeninae Siveter, 1977 and Calymeninae Milne-Edwards, 1840 and is paraphyletic with respect to the Colpocoryphinae; (3) the Flexicalymeninae is paraphyletic with respect to the Calymeninae and (4) the Homalonotidae Chapman, 1890 is monophyletic (see Figure 3.2). The trees differ in the relationships of *Dekalymene*, *Diacalymene* and *Spathacalymene*. One shows *Dekalymene* as closely-related to *Spathacalymene* and the other shows the three taxa as an unresolved trichotomy.

Specific relationships are discussed in the *Systematic Palaeontology* (section 3.5). Character states with ambiguous optimisation in this chapter are indicated by asterisks within the text below, next to the character in question.

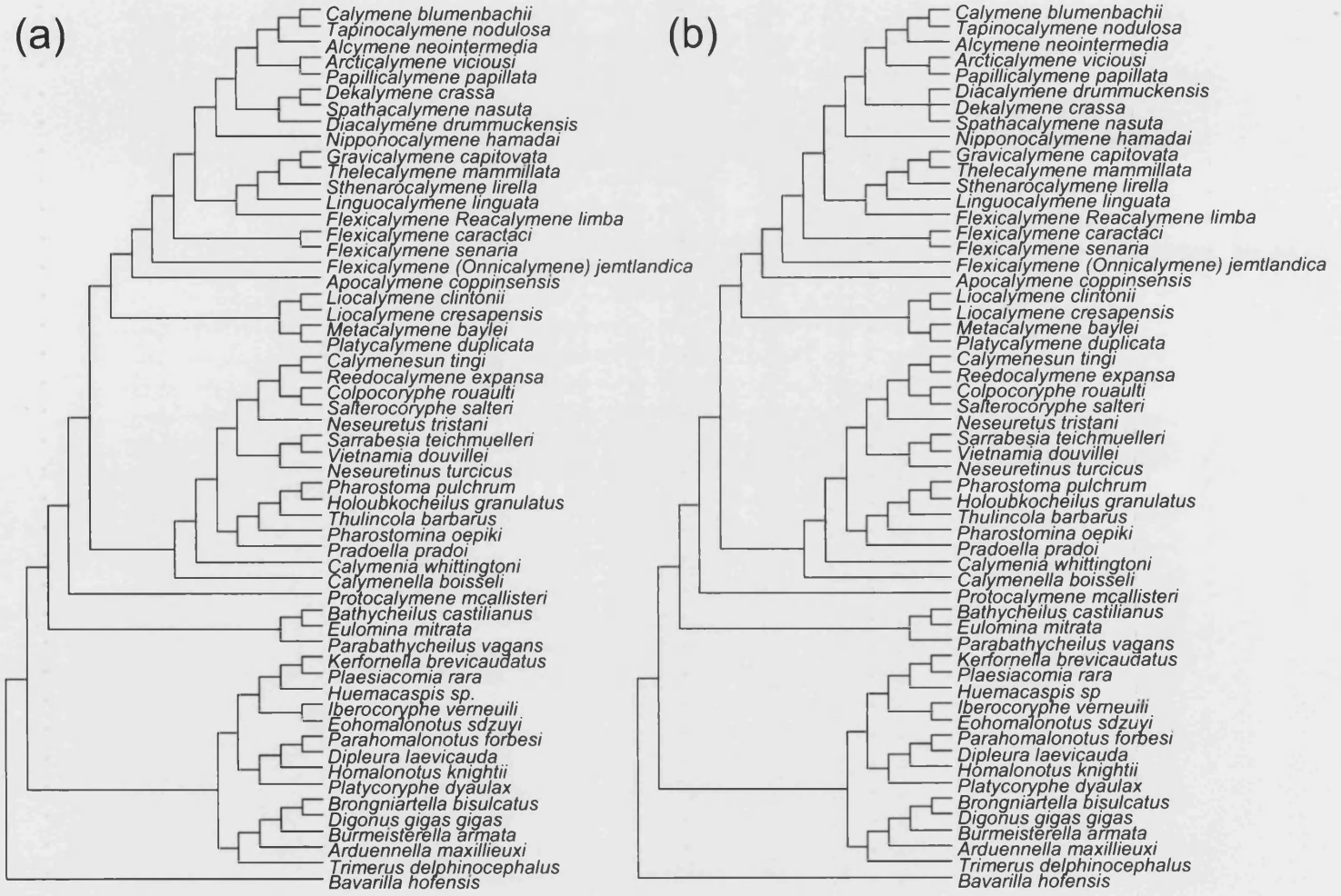

Figure 3.1: The two resulting MPTs from the analysis.

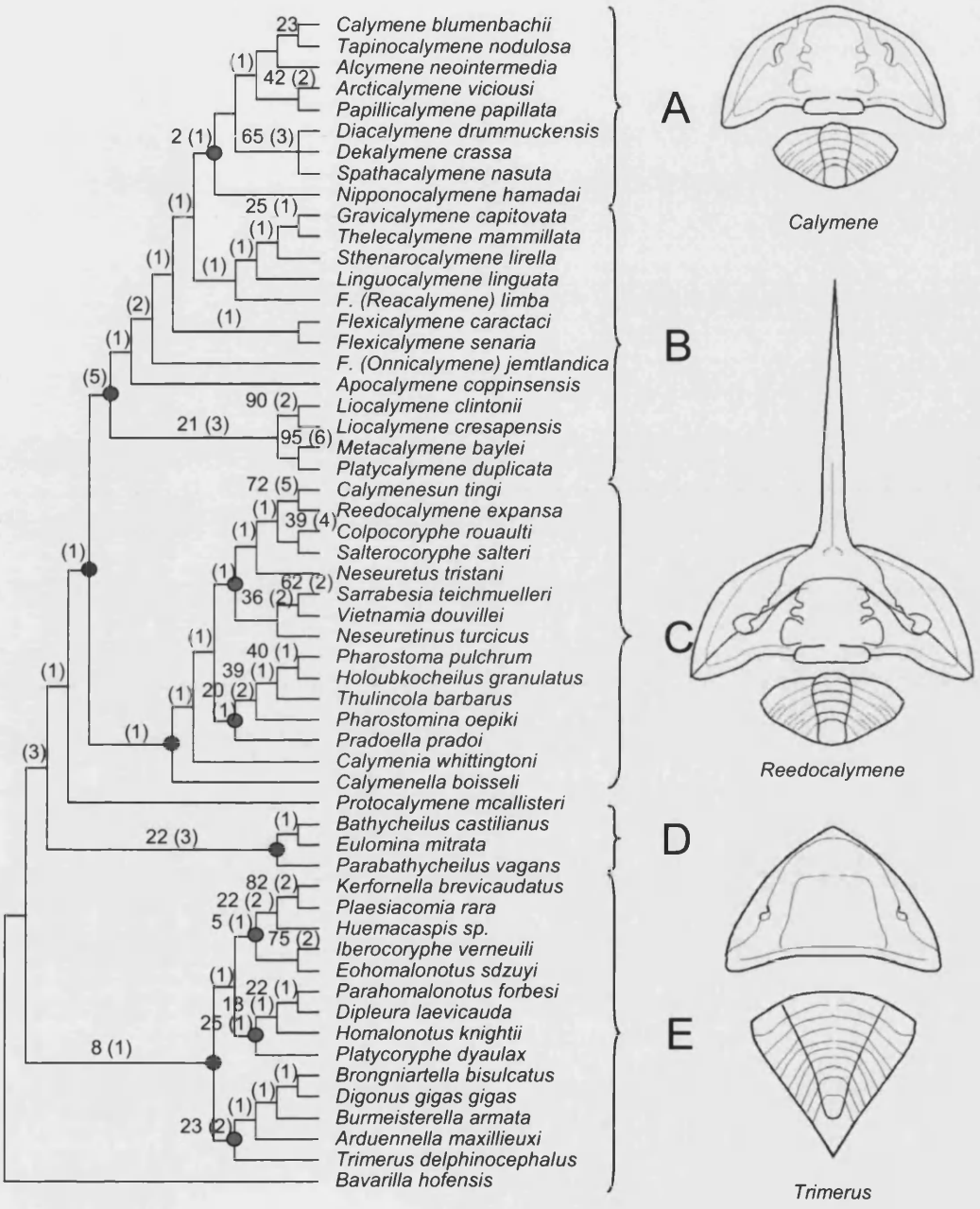
Calymene blumenbachii
Tapinocalymene nodulosa
Alcymene neointermedia
Arcticalymene viciousi
Papillicalymene papillata
Diacalymene drummuckensis
Dekalymene crassa
Spathacalymene nasuta
Nipponocalymene hamadai
Gravicalymene capitovata
Thelecalymene mammillata
Sthenarocalymene lirella
Linguocalymene linguata
F. (Reacalymene) limba
Flexicalymene caractaci
Flexicalymene senaria
F. (Onnicalymene) jemtlandica
Apocalymene coppinsensis
Liocalymene clintonii
Liocalymene cresapensis
Metacalymene baylei
Platycalymene duplicata
Calymenesun tingi
Reedocalymene expansa
Colpocoryphe rouaulti
Salterocoryphe salteri
Neseuretus tristani
Sarrabesia teichmuelleri
Vietnamia douvillei
Neseuretinus turcicus
Pharostoma pulchrum
Holoubkocheilus granulatus
Thulincola barbarus
Pharostomina oepiki
Pradoella pradoi
Calymenia whittingtoni
Calymenella boisseli
Protocalymene mcallisteri
Bathycheilus castilianus
Eulomina mitrata
Parabathycheilus vagans
Kerfornella brevicaudatus
Plaesiacomia rara
Huemacaspis sp.
Iberocoryphe verneuili
Eohomalonotus sdzuyi
Parahomalonotus forbesi
Dipleura laevicauda
Homalonotus knightii
Platycoryphe dyaulax
Brongniartella bisulcatus
Digonus gigas gigas
Burmeisterella armata
Arduennella maxillieuxi
Trimerus delphinocephalus
Bavarilla hofensis
A
B
C
D
E
Calymene
Reedocalymene
Trimerus

Figure 3.2: The 50% majority-rule tree from the analysis. A low cut-off limit was applied to the bootstrap values figured. Although it is acknowledged that often a bootstrap value of <50% is considered poor support for a node, it was felt important to convey the difference in support between the bootstrap support for other groupings. Bootstrap values and branch support values (given in adjacent brackets where >0) are shown above the branches. Clades A-E are indicated. Purple nodes delineate suprafamilal, green nodes delineate familial and red, subfamilial groupings.

3.4 DISCUSSION

It is interesting that the Calymenidae, as previously described, is paraphyletic in this analysis (Fig. 3.2, clades A and B). However, this proposed phylogeny fits into Shirley's model of division into two groups (1936, p. 392): (1) those species with an axial furrow that is not contracted and have no papillate lobes and (2) those with papillate lobes where the buttress develops from the sides of the fixigena over the axial furrows. It is possible that *Linguocalymene* has lost any buttresses, possibly having a paedomorphic origin as suggested for *Metacalymene* by Siveter (1979, p. 373). However, other characters of *Linguocalymene* are not reminiscent of the calymenines and constraining the tree so that it falls inside the clade of buttressed genera adds at least three steps to the tree length, making it a much less parsimonious proposal.

One of the MPTs is not fully resolved, which seems curious. But, it is acknowledged that polytomies can reflect actual phylogenetic patterns (the 'hard' polytomies of Maddison 1989) rather than reflecting only non-resolution. It is perhaps possible that an ancestral morphology survived a speciation event and then bifurcated again before acquiring any apomorphies (i.e. 'firm' polytomies; as suggested by Purvis & Garland 1993).

3.5 SYSTEMATIC PALAEONTOLOGY

Order **PHACOPIDA** Salter, 1864
Suborder **CALYMENINA** Swinnerton, 1915
Family **BAVARILLIDAE** Sdzuy, 1957

TAXA INCLUDED. *Bavarilla* Barrande, 1868.
STRATIGRAPHICAL RANGE. Lower to Upper Ordovician.

Family **HOMALONOTIDAE** Chapman, 1890

EMENDED DIAGNOSIS. Proparian facial suture (this suture is gonatoparian in some homalonotids, while some reeedocalymenines also have a proparian facial suture) (character (ch.) 5). Occipital tubercle absent (ch. 24*; homoplastic character state). Palpebral lobe opposite 2L (also seen in many calymenines and flexicalymenines) (ch. 27; homoplastic character state). Ratio of preocular fixed cheek to that of glabella at L2 is smaller or equal to a proportion of 0.4 (homoplastic character state) (ch. 28; homoplastic character state). Eye ridges absent (ch. 30*; homoplastic character state and present in *Iberocoryphe*, *Eohomalonotus* and *Brongniartella*). Anterior border is gently curved (ch. 42*; straight in some homalonotids). Occipital furrow that is shallow adaxially (homoplastic character state and reversed in some homalonotids) (ch. 47). Very shallow lateral border furrow on the librigena (homoplastic character state) (ch. 48). Librigenal spine absent (ch. 50*). Prominent maculae (homoplastic character state) (ch. 54). Pygidial border not defined by furrow (ch. 57*). Pygidium that is two-thirds or more as long as wide (homoplastic character state) (ch. 58). Five to nine pygidial axial ring furrows defined (ch. 59*).

TAXA INCLUDED. *Arduennella* Wenndorf, 1990; *Brongniartella* Reed, 1918; *Burmeisterella* Reed, 1918; *Digonus* Gürich, 1909; *Dipleura* Green, 1832; *Eohomalonotus* Reed, 1918; *Homalonotus* König, 1825; *Huemacaspis* Přibyl & Vaněk, 1980; *Iberocoryphe* Hammann, 1977; *Kerfornella* Henry, 1976; *Parahomalonotus* Reed, 1918; *Plaesiacomia* Hawle & Corda, 1847; *Platycorphe* Foerste, 1919; *Trimerus* Green, 1832.

STRATIGRAPHICAL RANGE. Middle Ordovician to Middle Devonian.

REMARKS. The Homalonotidae is monophyletic. Reed (1918) suggested that the Devonian taxa 'fall into two main groups': (1) *Parahomalonotus* and (2) a group composed of *Burmeisteria* Salter, 1865 and *Digonus* Gürich, 1909. *Burmeisteria* is not coded here but - assuming that *Burmeisteria* and *Burmeisterella* Salter 1965 are closely-related, this analysis suggests there are, indeed, two main groups: the eohomalonotids+homalonotids (*Parahomalonotus*) and trimerines (*Burmeisterella* and *Digonus*) decribed below.

Sufamily **EOHOMALONOTINAE** Hupé 1953

EMENDED DIAGNOSIS. Gonatoparian facial suture (ch. 5*; proparian in *Iberocoryphe*). Glabella displays severe anterior taping (ch. 9; but parabolic in *Huemacaspis*). Uniformly rounded glabella anterior margin (ch. 10*). Posterior border of glabella 'curls' anteriorly at lateral points (ch. 34*; straight in *Huemacaspis*). Anterior margin is longer (sag.) than the occipital ring (ch. 43). Eye socle absent (ch. 49*; known only in *Kerfornella*).

TAXA INCLUDED. *Eohomalonotus* Reed, 1918; *Huemacaspis* Přibyl & Vaněk, 1980; *Iberocoryphe* Hammann, 1977; *Kerfornella* Henry, 1976; *Plaesiacomia* Hawle & Corda, 1847.

STRATIGRAPHICAL RANGE. Middle Ordovician (Llanvirn - Llandeilo)

REMARKS. The close relationship between *Kerfornella* Henry, 1976, *Plaesiacomia* Hawle & Corda, 1847 and *Huemacaspis* Přibyl & Vaněk, 1980 is confirmed (the taxon 'Kerfornellinae' of Henry 1980. It is, however, expanded here to include *Eohomalonotus* and *Iberocoryphe* and so the taxon name Eohomalonotinae Hupé, 1953 has priority). Supporting apomorphies of these three taxa are (all homoplastic): (1) relatively smooth tuberculation (ch. 4); (2) absence of paraglabellar areas (ch.26*); (3) a distinctive vincular region (ch. 60); and (4) a smooth pygidial pleural area (ch. 62).

The grouping of *Colpocoryphe* and *Plaesiacomia* into the Colpocoryphinae by Vaněk (1965) seems to be based mainly on characters connected with enrollment (see Clarkson & Henry 1973). Indeed, those taxa are not shown to be closely-related here.

Sufamily **HOMALONOTINAE** Chapman, 1890

EMENDED DIAGNOSIS. Straight L1 furrow (ch. 14*; known only in *Platycoryphe*). Indistinct pygidial trilobation (ch. 64).

TAXA INCLUDED. *Dipleura* Green, 1832; *Homalonotus* König, 1825; *Parahomalonotus* Reed, 1918; *Platycorphe* Foerste, 1919.

STRATIGRAPHICAL RANGE. Mid Ordovician (Llanvirn) to Early Devonian (Lochkovian).

REMARKS. A close relationship between *Brongniartella* and *Platycoryphe* Foerste, 1919 (Whittington 1965; Thomas 1977) and also between *Trimerus* and *Dipleura* (Sdzuy 1959) is not supported; *Brongniartella* and *Trimerus* fall into one group (the Trimerinae below) and *Platycoryphe* and *Dipleura* into this grouping.

The Homalonotinae as defined by Thomas 1977 is paraphyletic: its taxa are divided here into two clades within clade E (the Homalonotinae and Trimerinae below).

Sufamily **TRIMERINAE** Hupé, 1953

EMENDED DIAGNOSIS. Pygidial length is subequal to the cephalon (ch. 3; exceeding cephalon length in *Digonus*). Triangular shaped frontal area of the cephalon as defined by anterior branches of facial suture (ch. 6; subparallel in *Brongniartella*). Distinct paraglabellar areas (ch. 26; absent in *Brongniartella*). Palpebral lobes shorter (sag.) than the occipital ring (ch. 29). Straight anterior border of cranidium (ch.42). Ten or more pygidial axial ring furrows (ch. 59). Postaxial ridge present on pygidium (ch. 61).

TAXA INCLUDED. *Arduennella* Wenndorf, 1990; *Brongniartella* Reed, 1918; *Burmeisterella* Reed, 1918; *Digonus* Gürich, 1909; *Trimerus* Green, 1832.

STRATIGRAPHICAL RANGE. Upper Ordovician (Longvillian) to Middle Devonian (Givetian).

REMARKS. The very close relationship between *Trimerus* Green, 1832 and *Brongniartella* Salter, 1865 is unfounded (Tomczykowa 1975).

Family **BATHYCHEILIDAE** Přibyl, 1953

EMENDED DIAGNOSIS. Anterior branch of facial sutures subparallel (ch. 6). Parabolic glabella (ch. 9*). Uniformly rounded anterior margin of glabella (ch. 10*). Curved L1 furrow (ch. 14*). Sagitally medially longer occipital ring (ch. 23*). Impressed occipital muscle pad (ch. 25). Palpebral lobe length is equal to that of the occipital ring (ch. 29). Fossulae present (ch. 31*). Preglabellar field present (ch. 38*). Fixigenal spine present (ch. 41). Low glabella (ch. 46*). 12 thoracic segments (ch. 55*; only known in

Bathycheilus). Complete interpleural and pleural furrows (ch. 62*). Distinct trilobation of the pygidium (ch. 64*).

TAXA INCLUDED. *Bathycheilus* Holub, 1908; *Eulomina* Růžička, 1931; *Parabathycheilus* Mergl, 1984.

STRATIGRAPHICAL RANGE. Lower to Upper Ordovician.

REMARKS. While the constituent subfamilies are monophyletic the family Bathcheilidae is polyphyletic in this analysis – the Pharostomatinae is closely-related to the Reedocalymeninae and the Bathycheilinae is basal to the Calymenidae. The placement of *Eulomina* within the Bathycheilidae seems sensible (see Mergl 1994).

Genus **PROTOCALYMENE** Ross, 1967
[*Subfamilia incertae sedis*]

TYPE SPECIES. *Protocalymene mcallisteri* Ross, 1967.

STRATIGRAPHICAL RANGE. Middle Ordovician.

REMARKS. In Turvey's study (2002a), *Protocalymene* is basal to *Bavarilla*. In the current study it is more derived, despite the latter taxon being selected as the outgroup in both studies. An explanation for this discrepancy could be that Turvey (2002a) coded *Protocalymene mcallisteri* as having a proparian facial suture and genal spines. However, these are immature characteristics: adult *Protocalymene* have a gonatoparian facial suture and no genal spines (see Ross 1967).

Superfamily **CALYMENOIDEA** Fortey *in* Kaesler, 1997

EMENDED DIAGNOSIS. Variously tuberculate ornamenation (ch. 4*). Gonatoparian facial suture (ch. 5*). Forked S1 (ch. 18). Articulation notch present (ch. 35). Anterior border length roughly equal to length (sag.) of occipital ring (ch. 43*). Pygidial border absent (ch. 57*).

TAXA INCLUDED. *Calymenella* Bergeron, 1890, *Calymenia* Kolobova *in* Sokolov & Ëlkin, 1978, families Reedocalymenidae Hupé, 1955 and Calymenidae Milne-Edwards, 1840.

STRATIGRAPHICAL RANGE. Lower Ordovician to Middle Devonian.

Genus ***CALYMENELLA*** Bergeron, 1890

[*Subfamilia incertae sedis*]

TAXA INCLUDED. *Calymenella* Bergeron, 1890.

STRATIGRAPHICAL RANGE. Lower to Upper Ordovician.

REMARKS. In this study, *Calymenella* Bergeron 1890 is basal to *Pharostomina* Sdzuy, 1955 (which is contained within the subfamily Pharostominae below). Turvey (2002a) supposed the converse relationship. But he coded *Calymenella preboisseli* Beckly, 1989 instead of the type species; this may account for the differences seen.

Calymenella Bergeron, 1890 has more affiliation with *Neseuretus*, as suggested by Hammann (1983), than with the Eohomalonotinae Hupé, 1953 (as supported by Hammann & Henry 1978).

The positions of *Protocalymene* (see above), *Pradoella* and *Calymenella* are dissimilar. *Pradoella* is basal to the bathycheilids here (see below) and *Calymenella* is basal to the bathycheilids and reedocalymines. In Turvey's study (2002a) these taxa were sister group to the *Neseuretus* group.

Genus ***CALYMENIA*** Kolobova *in* Sokolov & Ëlkin, 1978

[*Subfamilia incertae sedis*]

TAXA INCLUDED. *Calymenia* Kolobova *in* Sokolov & Ëlkin, 1978.

STRATIGRAPHICAL RANGE. Lower to Upper Ordovician.

REMARKS. *Calymenia* Kolobova *in* Sokolov & Ëlkin, 1978 was tentatively placed close to *Bathycheilus* by Hammann & Leone (1997) based on the shape of the glabella and the form of S1. This analysis suggests that *Calymenia* is actually more closely-related to the Pharostomatinae. Supporting apomorphies are: (1) two glabellar furrows, S3 indistinct (ch. 11); (2) a straight furrow defining L1 (ch. 14*); (3) the presence of distinct paraglabellar areas (ch. 26*) and (4) a weak articulation notch on the posterior cephalic margin (ch. 35).

Family **REEDOCALYMENIDAE** Hupé, 1955

Subfamily **PHAROSTOMINAE** Hupé 1953

EMENDED DIAGNOSIS. S1 shallowing abaxially (ch. 12). Forked S1 (ch. 18*). Ratio of preocular fixed cheek to that of glabella at L2 is smaller or equal to a proportion of 0.4 (ch. 28*). Presence of eye ridges (homoplastic character) (ch. 30). A broad point to the anterior border of the cranidium (reversed in some reedocalymenines) (ch. 42). An occipital furrow that is shallow adaxially (homoplastic character, seen in some homalonotids; ch. 47). A very shallow lateral border furrow on the librigena (homoplastic character, seen in some homalonotids; ch. 48). Absence of eye socle (ch. 49*). 'Pseudoborder' present (ch. 57). A pygidium that is two-thirds or more as long as wide (ch. 58). High convexity of pygidial axis (ch. 65).

TAXA INCLUDED. *Holoubkocheilus* Mergl, 1994*; Pharostomina* Sdzuy, 1955; *Pradoella* Hammann, 1977; *Pharostoma* Hawle & Corda, 1847; *Thulincola* Tripp, 1962.

STRATIGRAPHICAL RANGE. Early Ordovician (Tremadoc) to Middle Ordovician (Llandeilo).

REMARKS. *Holoubkocheilus*, *Pharostomina*, *Pharostoma* and *Thulincola* should be included in the subfamily Pharostomatinae Hupé 1953, as suggested by earlier workers (e.g. Tripp 1962; Mergl 1994). However, the subfamily should be expanded to incorporate *Pradoella*.

Subfamily **REEDOCALYMENINAE** Hupé, 1955

EMENDED DIAGNOSIS. Impressed occipital muscle pad (ch. 25*). A lens-like posterior border furrow (homoplastic character state) (ch. 33). An inflated preglabellar field (ch.40*). A post-axial ridge (homoplastic character state) (ch. 61).

TAXA INCLUDED. *Calymenesun* Kobayashi, 1951; *Colpocoryphe* Novak *in* Perner, 1918; *Neseuretinus* Dean, 1967; *Neseuretus* Hicks, 1873; R*eedocalymene* Kobayashi, 1951; *Salterocoryphe* Hammann, 1977; *Sarrabesia* Hammann & Leone, 1997*; Vietnamia* Kobayashi, 1960.

STRATIGRAPHICAL RANGE. Early Ordovician (Tremadoc) to Late Ordovician (Ashgill).

REMARKS. The analysis confirms that *Calymensun* and *Reedocalymene* are sister-groups (see Lu 1975; Zhou *et al.* 1984; Peng *et al.* 2000).

The results confirm the close relationship between *Salterocoryphe* and *Colpocoryphe* and places both among the reedocalymenines (as suggested by Hammann 1983, p. 79) rather than with the Kerfornellinae Henry, 1980 (as supposed by Hammann & Leone 1997) or the Flexicalymenine (*Salterocoryphe*; as supposed by Henry 1980). The former Colpocoryphinae are grouped specifically with *Reedocalymene expansa* Yi, 1957 and *Calymensun tingi* (Sun 1931) because of the presence of: (1) paraglabellar areas present in furrows (ch. 26*); (2) preglabellar field that is not inflated (ch. 40*); (3) an eye socle (a reversal) (ch. 49); (2) vincular furrows on the pygidium (homoplastic character) (ch. 60). *Colpocoryphe* and *Salterocoryphe* are grouped together by: (1) the absence of fossulae (seen also in the Homalonotidae and *Bavarilla*) (ch. 31); (2) a marked angular deflection of the posterior cephalic margin (seen in the calymenines and flexicalymenines) (ch. 35); (3) the absence of a preglabellar field (seen in the calymenines, flexicalymenines and homalonotids) (ch. 38) and (4) normal pleural furrows present but no interpleural ones (ch. 62*); and (5) a highly convex pygidial axis (seen in some calymenines, flexicalymenines and bathychelines) (ch. 66).

Sarrabesia Kobayashi, 1960 and *Vietnamia* Kobayashi, 1960 are closely-related, but display many differences (see Hammann & Leone 1997, p. 118) so should not be thought of as congeneric as supposed by Turvey (2002a).

Resulting relationships between the reedocalymenines here are identical with those obtained by Turvey (2002b) using a different character list.

Family **CALYMENIDAE** Milne-Edwards, 1840

EMENDED DIAGNOSIS. L1 separated from median lobe by furrow (ch. 15). Curved L1 (ch. 14*). Forked S1 (ch. 18*). Articulation notch is distinct (ch. 35). Anterior border margin present (ch. 37). Preglabellar field absent (ch. 38). Preglabellar not gently sloping (either roll-like or with ridge; ch. 39). Preglabellar furrow present and deep (ch. 45). Occipital furrow strongly imprinted across with no shallowing adaxially (ch. 47).

TAXA INCLUDED. 'Grade' Flexicalymeninae Siveter, 1976 and subfamily Calymeninae Milne-Edwards, 1840.

STRATIGRAPHICAL RANGE. Lower Ordovician to Middle Devonian.

'Grade' **FLEXICALYMENINAE** Siveter, 1976

TAXA INCLUDED. *Apocalymene* Chatterton & Campbell, 1980; *Flexicalymene* Shirley, 1936; *Flexicalymene (Onnicalymene)* Dean, 1962; *Flexicalymene (Reacalymene)* Shirley, 1936; *Gravicalymene* Shirley, 1936; *Linguocalymene* Tomczykova, 1991; *Liocalymene* Raymond, 1916; *Metacalymene* Kegel, 1927; *Platycalymene* Shirley, 1936; *Sthenarocalymene* Siveter, 1977; *Thelecalymene* Whittington, 1971b.

STRATIGRAPHICAL RANGE. Middle Ordovician (Llanvirn) to Late Silurian (Ludlow).

REMARKS. The group is explicitly paraphyletic and displays the following characteristics:

- *Thelecalymene* Whittington 1971a is, indeed, closely-related to *Gravicalymene* Shirley 1936 (see Whittington 1971a): (1) three glabellar furrows (ch. 11*); (2) L1 is greater in length (sag.) than L2 plus L3 (ch. 13); and (3) absence of fossula (ch.31).
- *Sthenarocalymene* Siveter, 1977 is more closely related to *Gravicalymene*, as thought by Siveter (1977, p. 386), than it is to *Flexicalymene* Shirley 1936.
- *Recalymene* and *Onnicalymene* are both closely-related to *Flexicalymene s.s.* but neither should be included within the latter genus (see Siveter 1977).
- *Recalymene* is more closely-related to other flexicalymenines than *Flexicalymene* s.s.
- *Metacalymene* Kegel, 1927 is closely-related to *Platycalymene* Shirley, 1936 as suggested by previous workers (Barrande 1852; Shirley 1936; Whittard 1960; Siveter 1979). The argument that homeomorphy is responsible for the resemblance of *Metacalymene* to *Platycalymene* seems unfounded here (see Shirley 1936; Hughes 1969).
- The relationship of *Liocalymene* Raymond, 1916 to other taxa is obscure (Whittington 1971b, p. 474) but it is seen here as closely-related to *Metacalymene* and *Platycalymene*. Supporting apomorphies for this relationship are: (1) the same body proportions (ch. 1); cephalic length to body ratio (ch. 2); (3) cephalic and pygidial length are roughly the same (ch. 3); (4) L1 separated from median lobe (ch. 15*); (5) no paraglabellar areas (ch. 26*); (6) weak deflection of posterior cephalic margin (ch. 35*); (7) this deflection is less than half the transverse width of the occipital ring (ch. 36*); (8) anterior adaxial margin is rounded (ch. 37*); (9) no preglabellar field (ch. 38*); (10) short preglabellar

area (ch. 39*); (11) anterior border length is less than that of the occipital ring (ch. 43) and (12) a deep preglabellar furrow (ch. 45*).

- Things that group *Liocalymene*, *Metacalymene* and *Platycalymene* with taxa within the clades C, D, and E are: (1) transversely elongate L2 (ch. 17); (2) L3 not independent of glabella (ch. 22) and (3) low convexity of pygidial axis (ch. 65).
- *Apocalymene* is not synonymous with *Sthenarocalymene* as suggested by Holloway (1980). Several differences are apparent between the two genera: (1) *Sthenarocalymene* has a sigmoidal postocular suture without an outwards turn, that of *Apocalymene* has an outwards turn (ch. 7); (2) *Sthenarocalymene* has a transverse anterior cranidial margin, that of *Apocalymene* is gently rounded (ch. 10); (3) *Sthenarocalymene* has a 4p furrow (albeit small but well-defined), *Apocalymene* has 2p furrow and an indistinct 3p (ch. 11); (4) the 2p lobe of *Sthenarocalymene* is not separated from the medial glabellar lobe, however that of *Apocalymene* is (Chatterton & Campbell (1980) state that '1p and 2p [are] not tending to become isolated' but a distinct furrow, as defined in this study, can be seen in, for example, their plate 8, figure 18) (ch. 16); (5) some *Sthenarocalymene sp.* have a small occipital node, *Apocalymene* never do (ch.24); (6) the palpebral lobe of *Sthenarocalymene* is opposite 2L, that of *Apocalymene* are opposite 2S/3L (ch. 27); (7) *Sthenarocalymene* has an eye ridge, *Apocalymene* does not (ch. 30); (8) *Sthenarocalymene* has a weak articulation notch on posterior cephalic margin, that of *Apocalymene* is better defined (ch. 35); (9) the anterior adaxial margin of the preocular fixigena of *Sthenarocalymene* are pointed and overhanging anterior border furrow, *Apocalymene* preocular fixigena do not overhang the anterior border furrow (ch. 37); (10) *Sthenarocalymene* has a subtransverse ridge on the preglabellar area, whereas that of *Apocalymene* is more roll-like (ch. 39) and (11) the anterior border length of *Sthenarocalymene* is less than that of the occipital ring, that of *Apocalymene* is about equal (ch. 43). It is recognized that the distinction made between these two genera are essentially small differences in the expression of only some characters. However, this is an instance of genera being distinct based on character combinations rather than a few characters states that are thought to be individually diagnostic (see Holloway 1980, p.58).
- *Gravicalymene*, *Thelecalymene*, *Sthenarocalymene*, *Linguocalymene* and *Reacalymene* are grouped by: (1) sigmoidal postocular suture without outwards

turn (ch. 7); (2) bell-shaped glabella (ch. 9*); (3) subtransverse ridge on preglabellar area (ch. 39); and (4) developed lateral lobes on axial rings (ch. 56*).

Subfamily **CALYMENINAE** Milne-Edwards, 1840

EMENDED DIAGNOSIS. Bell-shaped glabella (ch. 9). Buttressed L2 (ch. 20). Hypostomal rhynchos present (doubled in *Nippocalymene*; ch. 53).

TAXA INCLUDED. *Alcymene* Ramsköld *et al.*, 1994; *Arcticalymene* Adrain & Edgecombe, 1997; *Calymene* Brongniart, 1822; *Dekalymene* Curtis & Lane, 1998; *Diacalymene* Kegel, 1927; *Nipponocalymene* Kaneko, 1985; *Papillicalymene* Shirley, 1936; *Spathacalymene* Tillman, 1960; *Tapinocalymene* Siveter, 1980.

STRATIGRAPHICAL RANGE. Early Silurian (Llandovery) to Middle Devonian (Givetian).

REMARKS. This subfamily is monophyletic and shows the following relationships:

- The close relationship between *Tapinocalymene* Siveter, 1980, *Diacalymene* Kegel, 1927 and *Calymene* Brongniart, 1822 is supported (see Siveter 1980).
- *Arcticalymene* Adrain & Edgecombe, 1997 and *Papillicalymene* Shirley, 1936 are resolved here as sister-groups – an argument that these taxa are unrelated and that common character states are homoplastic (see Siveter & Chatterton 1996) is not supported. They share: (1) four glabellar furrows (ch. 11*); (2) buttressed form of L3 (ch. 21); (3) an articulating point more than half width of occipital ring (ch. 36); (4) an anterior border shorter (sag.) than occipital ring (ch. 43*); (5) a pygidium that is two-thirds or more as long as wide (ch. 58) and (6) interpleural furrows that are present only abaxially, accompanied by flared pleural furrows (ch. 62).
- *Dekalymene* is closely-related to *Diacalymene* (Siveter, *pers. comm.*) and perhaps should not have generic status. *Dekalymene* differs in the following characteristics from *Diacalymene*: (1) uniformly rounded anterior margin of glabella rather than transverse (ch. 10); (2) 1S not shallowing abaxially (ch. 12) and (3) L3 is independent of glabella (ch. 22).
- There is a strong case for the suppression of *Spathacalymene* as it forms an unresolved trichotomy with *Decalymene* and *Diacalymene* (supported by recent unpublished fossil finds of calymenids that possess the subtransverse ridge of the preglabellar area of *Diacalymene*, with preglabellar fields longer than *Diacalymene* and not as long as *Spathacalymene*; Edgecombe, *pers. comm.*).

- *Alcymene* is indeed closely-related to *Calymene* (Ramsköld *et al.* 1994).

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4. The phylogeny and disparity of the Odontopleurida (Trilobita)

4.1 INTRODUCTION

THE Odontopleurida Whittington, 1959 is thought to have a close affinity with the Lichida (see Chapter 2 and Tripp & Evitt 1981); indeed, both of these groups are placed within the same order by some workers (see Fortey 2001; Thomas & Holloway 1988). The former is well-represented by a wealth of exquisitely preserved, silicified faunas (e.g. Whittington 1956a; Chatterton & Perry 1983) and, thus, is known in rich morphological detail. Being a character-rich group it is ideal for phylogenetic analysis. Furthermore, the group displays a wide range of apparently disparate morphologies. Is the disparity of odontopleurid clades consistent through their stratigraphic record? How does the disparity pattern compare to that of other trilobite families, for example, those of the Illaenoidea Hawle & Corda, 1847?

Well-preserved odontopleurid material was first described by Barrande around 150 years ago (1852, 1872) and later re-described by Prantl and Přibyl (1949). Exceptionally silicified, well-preserved Middle Ordovician material from north Virginia, USA, was described in detail by Whittington (1956a; see Plate 4 overleaf).

At present, six odontopleurid families are accepted: Acidaspidinae Salter, 1864; Apianurinae Whittington, 1956a; Ceratocephalinae Richter & Richter, 1925; Koneprusiinae Vanêk & Pek, 1987; Odontopleurinae Burmeister, 1843 and Selenopeltinae Hawle & Corda, 1847 (see Plate 5 (a-f) for examples).

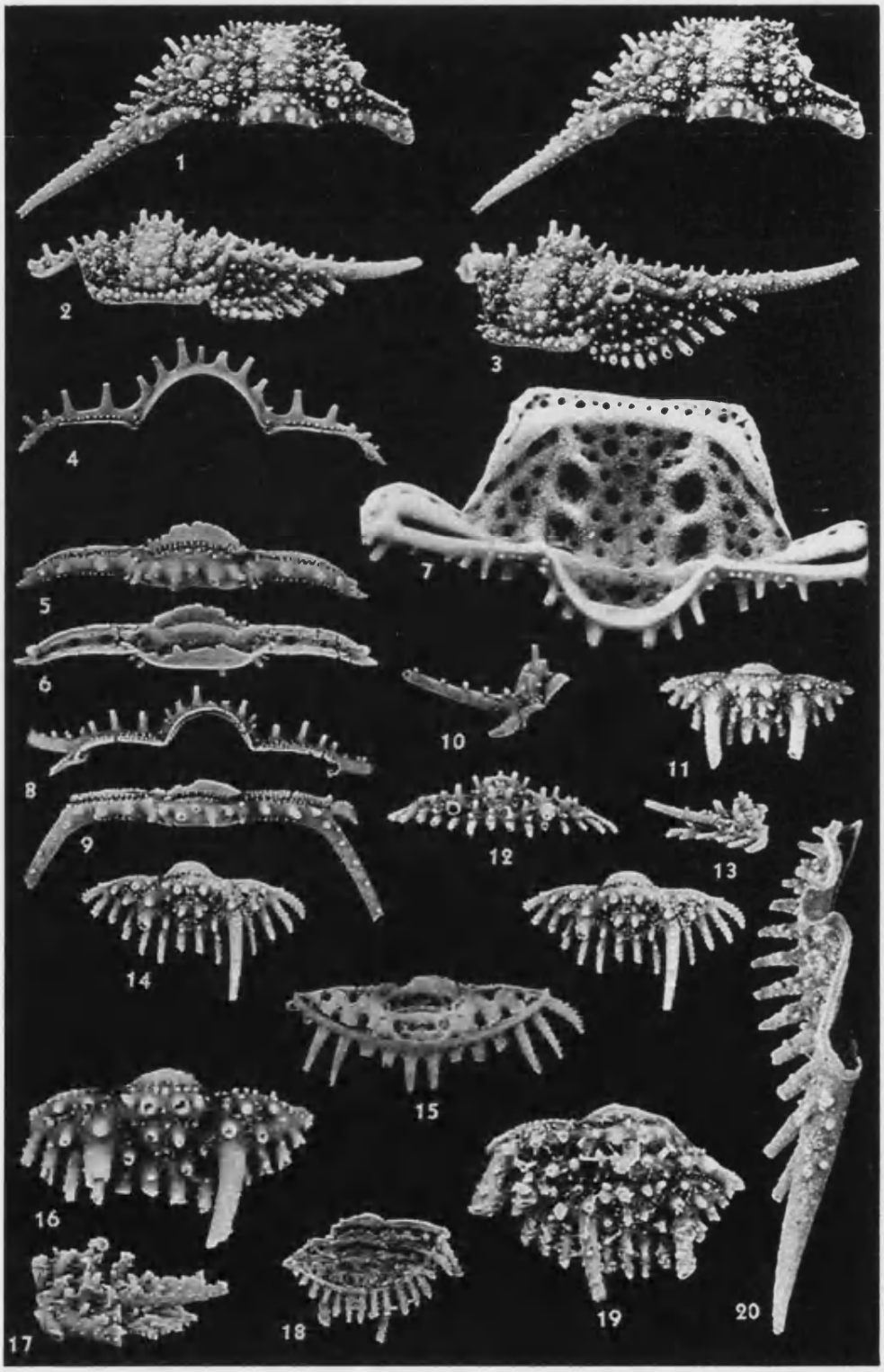

Plate 4

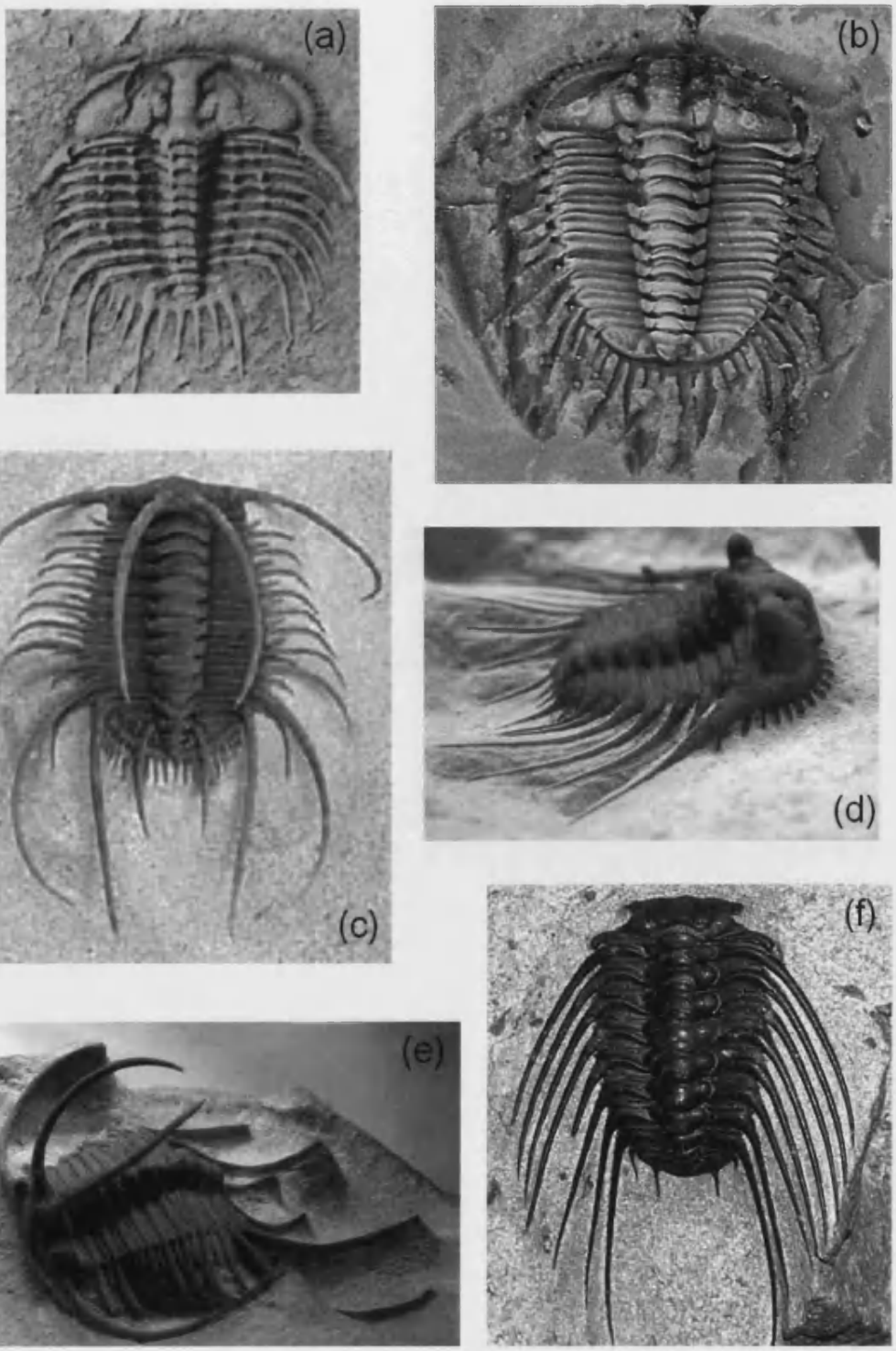

Plate 5

Plate 4.
Silificied trilobites (plate 12 of Whittington 1956); x 1.25.

Plate 5.
(a) *Sinespinaspis markhami* Edgecombe & Sherwin, 2001, Fig. 4(b); x 5.0; (b) *Dudleyaspis bowningensis* (http://www.austmus.gov.au/palaeontology/collections/trilobites.htm), x 5.0; (c) *Acidaspis* sp. (www.fossilien.de); x 2.0; (d) *Kettneraspis* sp. (www.thefossilmuseum.net); x. 4.0; (e) *Boedaspis ensifer* (www.fossilmall.com); x 4.0; (f) *Selenopeltis* (www.trilobita.de); x 0.75).

4.2 PHYLOGENETIC ANALYSIS

4.2.1 TAXONOMIC SAMPLING

Given the broad scope of this study, character state assignments were determined primarily on the basis of published descriptions and illustrations. In general, type species were coded. However if these were poorly known, better-preserved congeneric species were coded instead. All taxa included in the analysis are listed in Table 4.1 below; authorship and important subsequent references are also given.

Several taxa were excluded as they were extremely poorly-documented and/or poorly known, and obscured resolution among the remaining taxa. These taxa are: *Archaeopleura* Ramsköld, 1991b; *Brutonaspis* Pek & Vaněk, 1991; *Eoleonaspis* Sheng, 1974; *Meadowtownella* Přibyl & Vaněk, 1965; *Ningnanaspis* Sheng, 1974; *Orphanaspis* Prantl & Přibyl, 1949; *Periallaspis* Bruton, 1966b and *Elbaspis* Baldis & Blasco, 1973.

4.2.2 METHODS

See section 3.3.2 for full description of methods (i.e. PTP tests, bootstrapping, the use of ACCTRAN, TreeRot and MacClade). The dataset from Appendix II was analyzed using PAUP (version 4.0b10*, Swofford 2002). All characters were equally weighted and treated as unordered. The dataset includes no autapomorphies or phylogenetically-uninformative characters.

It is well known that different characters in a dataset can support different clades or nodes. This property can be useful: various sub-sets of characters can be used to construct different trees that, in turn, can each be used as a starting point in a tree

Genus	Coded Species	Author & publication year
Acanthalomina	*minuta*	Prantl & Přibyl 1949
Acidaspis	*brightii*	Murchison 1839 (Chatterton & Perry 1983)
Anacaenaspis	*gotlandensis*	Bruton 1967 (Ramsköld 1984)
Apianurus	*barbatus*	Whittington 1956a (Bruton 1966b)
Boedaspis	*ensifer*	Whittington & Bohlin 1958 (Bruton 1966b)
Borkopleura	*gorella*	Šnajdr 1984a
Calipernurus	*insolitus*	Whittington 1956a
Ceratocara	*Ceratocephala rarispina* Whittington, 1956a	Ramsköld 1991b (Prantl & Přibyl 1949)
Ceratocephala	*goniata* (supplemented with information from *C.laciniata* Whittington & Evitt, 1954)	Warder 1838 (Whittington & Evitt 1954; Chatterton & Perry 1983; Holloway 1994)
Ceratocephalina	*tridens*	Whittington 1956 (Chatterton & Perry 1983)
Ceratonurus	*Acidaspis krejcii* Prantl & Přibyl, 1949	Novák 1883 (Prantl & Přibyl 1949)
Chlustinia	*Acidaspis keyserlingi* Barrande, 1846	Přibyl & Vaněk 1965
Dalaspis	*Acidaspis (Dalaspis) drzymlai*	Chatterton & Perry 1983
Diacanthaspis	*cooperi*	Whittington 1941 (Prantl & Přibyl 1949; Chatterton & Perry 1983)
Dicranurus	*Acidaspis hamata* Hall, 1859	Conrad 1841 (Prantl & Přibyl 1949)
Dudleyaspis	*Acidaspis quinquespinosa* Lake, 1896	Prantl & Přibyl 1949 (Chatterton & Perry 1983; Ramsköld 1984)
Edgecombeaspis	*johansonae*	Adrain & Ramsköld 1997
Exallaspis	*Leonaspis bufo* Ramsköld, 1984	Bruton 1967 (some *Leonaspis* sp. designated to *Exallaspis* by Ramsköld & Chatterton 1991; Ramsköld 1991b)
Gaotania	*ovata*	W. Zhang 1974 (Holloway 1994)
Globulaspis	*Acidaspis (Globulaspis) prominens*	Reed 1931
Gondwanaspis	*mrirtensis*	Feist 2002
Hispaniaspis	*Diacanthaspis morenaica* Hammann, 1976	Hammann 1992
Isoprusia	*mydlakia*	Bruton 1966a (Ramsköld 1991a)

Ivanopleura	*Odontopleura dufrenoyi* Barrande, 1846	Šnajdr 1984a (Adrain & Chatterton 1990)
Kettneraspis	*Acidaspis pigra* Barrande, 1872	Prantl & Přibyl 1949 (Ramsköld 1991b; Adrain & Ramsköld 1997)
Koneprusia	*Acidaspis fuscina* Novák, 1883	Prantl & Přibyl 1949 (Ormiston 1969)
Laethoprusia	*salax*	Ramsköld 1991a
Leonaspis	*Odontopleura leonhardi* Barrande, 1846	Richter & Richter 1917 (Chatterton & Perry 1983; Ramsköld 1984, 1991b; Siveter 1989)
Miraspis	*Odontopleura mira* Barrande, 1846	Richter & Richter 1917 (Prantl & Přibyl 1949; Bruton 1966b)
Odontopleura	*ovata*	Emmrich 1839 (Chatterton & Perry 1983; Šnajdr 1984b; Adrain & Chatterton 1990)
Primaspis	*Odontopleura primordialis* Barrande, 1846	Richter & Richter 1917 (Bruton 1966b; Romano 1982; Chatterton & Perry 1983; Siveter 1989)
Proceratocephala	*Acidaspis terribilis* Reed, 1914	Prantl & Přibyl 1949 (Ramsköld 1991b)
Radiaspis	*Arges radiatus* Goldfuss, 1843	Richter & Richter 1917 (Prantl & Přibyl 1949
Rinconaspis	*santiaguensis*	Baldis & González 1918
Selenopeltis	*Odontopleura buchii* Barrande, 1846	Hawle & Corda 1847 (Prantl & Přibyl 1949; Dean 1966; Bruton & Henry 1978; Romano 1982; Hammann *et al.* 1986)
Selenopeltoides	*Acidaspis hawlei* Barrande 1852	Prantl & Přibyl 1949
Sinespinaspis	*Odontopleura greenwoodi* Chatterton & Perry, 1983	Adrain & Chatterton 1990 (Edgecombe & Sherwin 2001)
Snoderaspis	*krausi*	Ramsköld 1984
Stelckaspis	*warreni*	Chatterton & Perry 1983
Taemasaspis	*Primaspis (Taemasaspis) campbelli*	Chatterton 1971
Uriarra	*kausi*	Chatterton & Campbell 1980
Whittingtonia	*Acidaspis bispinosus* McCoy 1846	Prantl & Přibyl 1949 (Bruton 1966b; Price 1980)

Table 4.1: A list of all taxa included in the analysis. References are given for type species; other important literature is referenced in brackets.

search. This prevents the search becoming over-concentrated on a limited set of trees during the process and increases the overall effectiveness of a search (i.e. prevents the computer search becoming 'stuck' in local optima of similar cladograms; see Maddison 1991). Such a method is employed here: it is known as the *parsimony ratchet* (Nixon 1999). The methodology of the ratchet is summarized below but full details are given in Nixon (1999).

A starting tree is built in the same way as when a heuristic search is employed. Then 5-25% of the characters in the given dataset are randomly selected and emphasised by increasing the weight of these characters (in this case, simply by duplicating the characters in the dataset). A second tree is constructed from the modified dataset. The second tree is used to search from the starting tree (by tree bisection and reconnection) using the original, unweighted complement of characters (see Felsenstein 2004, p. 51-52). Each ratchet batch instructed 200 iterations; and 20 batches were executed. All 4000 trees were then read back into PAUP excluding any replicate trees. Finally, the trees were filtered to isolate only those with the shortest length.

4.2.2.1 Outgroup

The oldest known odontopleurid is arguably the Asian genus *Eodontopleura* Qian & Lin 1974 *in* Zhang *et al.* 1980, which is known only from a poorly-preserved cranidium. This genus was originally coded into the analysis but provided such a low level of information as a key-taxon that it was deemed appropriate to exclude it in preference for another, better-preserved taxon.

Selenopeltis was selected because it is a well-preserved, stratigraphically-old taxon and displays several primitive features such as: (1) an anterior facial suture that is inclined to the axis (ch. 26); (2) sub-genal notch (ch. 31); (3) broad and shallow middle furrow on hypostome (ch. 34); (4) inflated antero-lateral part of the thoracic axial ring (ch. 43) and (5) 6 pairs of exterior pygidial border spines (ch. 51).

4.2.2.2 Characters

The terminology of the *Treatise on Invertebrate Paleontology* (Moore 1997) is followed throughout this study unless otherwise stated. Some odontopleurid ontogenies are known (Table 4.2):

Taxon	**Paper(s) that describe ontogenetic stages**
Leonaspis (referred to *Ketteraspis* in Ramsköld 1991a)	Whittington & Campbell 1967; Chatterton 1971; Chatterton & Perry 1983
Taemasaspis campbelli	Chatterton 1971
Ceratocephala vexilla	Whittington & Evitt 1954; Chatterton 1971; Whittington 1956a
*Radiaspis bispinosus**	Chatterton 1971
*Ceratocephalina**	Chatterton 1980
Diacanthaspis	Whittington 1956b; Hu 1974
*Primaspis**	Whittington 1956a
*Acidaspis**	Chatterton & Perry 1983
*Dudleyaspis**	Chatterton 1971
Exallaspis	Schrank 1969; Schöning 1986
Apianurus	Chatterton 1980
Ceratocara	Chatterton *et al.* 1997

Table 4.2: Known odontopleurid ontogenies. Asterisked taxa did not provide informative codable information here.

The character number in the following list corresponds directly to its number in the dataset (Appendix II). References given after characters relate to relevant papers; character numbers given relate to those characters that are discussed in the given reference.

Cranidium

1. Anterior cranidial border (Ramsköld 1991b, character (ch.) 1):
    0. Wide, granulated/tuberculated
    1. Narrow/smooth

2. Anterior border tubercles (Ramsköld & Chatterton 1991, ch. 1):
    0. Absent, smooth

1. Single row of 10-20 symmetrically-set tubercles
2. Numerous, irregular rows of tubercles
3. Expressed as spines, e.g. *Gondwanaspis*

3. Glabellar topology around spine pair three (Ramsköld 1991b, ch. 2):
   0. Area around base of spines is not inflated
   1. Area around base of spines is inflated and stands above adjacent areas, e.g. *Ceratocephala*

4. Definition of L3 by S2 and S3 (Ramsköld 1991b, ch. 4):
   0. L3 defined (S3 distinct)
   1. L3 absent (S3 not impressed or rudimentary)

5. Tubercles A1, A2, A3 relative to other tubercles on the fixigena (Ramsköld 1991b, ch. 5). This terminology follows Whittington (1956a, p.161):
   0. Of similar size
   1. Much larger than other tubercles

6. Glabellar tubercle pairs 2, 3 and 4 retained into adult stages:
   0. Absent, indistinguishable from accessory glabellar spines and tubercles, e.g. *Odontopleura*
   1. Present, e.g. *Edgecombaspis*

7. Posterior border furrow laterally (Ramsköld 1991b, ch. 5):
   0. Furrow continues unbroken onto free cheek
   1. Furrow curves anterolaterally and merges with palpebral furrow; strong sutural ridge runs from posterior border to eye, i.e. *Ceratocara*, *Ceratocephala*, *Ceratonurus* and *Proceratocephala*

8. Median occipital tubercle (Ramsköld 1991b, ch. 7; Chatterton *et al.* 1997):
   0. Absent
   1. Present as a rounded projection
   2. Present as a spine, i.e. a projection that tapers outward, the length being greater than the width at the base

9. Occipital tubercle bearing four pits arranged at the corners of a square (occipital organ):
    0. Absent
    1. Present, e.g. *Kettneraspis caldwelli*, *Gondwanaspis*

10. Paired occipital spine (Ramsköld 1991b, ch. 8):
    0. Present
    1. Absent

11. Posterior margin of occipital ring produced backwards into form of stout median spine:
    0. Absent
    1. Present, e.g. *Acidaspis*

12. Condition of O_{ap} spines (Adrain & Chatterton 1990, ch. 8):
    0. Spines absent
    1. Present and distinctly posterior to median occipital spine/tubercle
    2. Present and approximately lateral to median occipital spine/tubercle

13. Height of eye (Ramsköld 1991b, ch. 10):
    0. Low
    1. Eye lobe elevated, eye set on short, thick stalk, e.g. *Acidaspis*
    2. Set on long stalk, e.g. *Miraspis*

14. Depth of longitudinal glabellar furrows (Chatterton *et al.* 1997, ch. 9):
    0. Shallow
    1. Deep

15. Posterior band on occipital ring (Chatterton *et al.* 1997, ch. 10):
    0. Distinct
    1. Absent or inconspicuous

16. Occipital lobes of occipital ring (Adrain & Chatterton 1990, ch. 4):
    0. Absent

1. Weakly defined
2. Strongly defined

17. Depth of occipital furrow (Chatterton *et al.* 1997, ch. 11; Adrain & Chatterton 1990):
    0. Sharp and deep
    1. Shallow and broad
    2. Shallow medially

18. Orientation of occipital spine pairs (Chatterton *et al.* 1997, ch. 12):
    0. Curved inwards or backwards distally
    1. Curved outwards distally

19. Width of fixigena (Chatterton *et al.* 1997, ch. 13):
    0. Narrow (opposite eye width less than or equal to maximum width of L1)
    1. Broad (wider opposite eye than maxiumum width of L1)

20. Anterior margin of crandium (Chatterton *et al.* 1997, ch. 16):
    0. Straight/transverse
    1. Curved into three convex forward lobes: anterior margin with median and lateral bulges, e.g. *Acidaspis* and *Dudleyaspis*

21. Glabellar ornament:
    0. Slim, thorn-like spines and small tubercles
    1. Large flattened tubercles
    2. Granular

22. Antennular notch:
    0. Deep
    1. Shallow or indistinct

23. Glabella widest across:
    0. Posterior part of L1
    1. Anterior part of L1

2. Subrectangular/parallel-sided, e.g. *Gondwanaspis*/*Dudleyaspis*

24. Position of eyes:
    0. Opposite anterior part of L1
    1. Opposite posterior part of L1

25. Functioning facial suture in the holaspid stage (Chatterton & Perry 1983, p. 32):
    0. Present
    1. Absent, e.g. *Acidaspis*, *Stelckaspis*, *Anacaenaspis*

26. Course of anterior facial suture (Reed 1925):
    0. Parallel to axis
    1. Inclined to axis

Librigena

27. Border spines of librigenae (Ramsköld 1991b, ch. 12):
    0. Prominent, elongate border spines present
    1. Border spines tiny
    2. Border spines absent

28. Orientation of genal spines:
    0. Genal spines not downwards-directed in a vertical plane
    1. A row of almost vertically downwards-directed spines, e.g. many acidaspines

29. Border spines (Ramsköld & Chatterton 1991, ch. 16):
    0. 10-11
    1. 12-13
    2. 14-15
    3. 16 or more

30. Direction of librigenal spine:
    0. Directed horizontally, backward and outward, e.g. Odontopleuridae

1. Directed upwardly, e.g. Apianurinae and Miraspininae

31. Sub-genal notch:
    0. Absent (librigenal spine low on cephalon)
    1. Present (librigenal spine high on cephalon)

32. Posterior sutural ridge developed along posterior facial suture on librigena:
    0. Absent, e.g. *Anacaenaspis* (see Bruton 1967, p. 235)
    1. Present, e.g. *Acidaspis*, *Sinespinaspis*

Hypostome

33. Outline:
    0. Slightly wider than long (e.g. odontopleurids and *Selenopeltis*)
    1. Widest anteriorly, e.g. Apianurinae
    2. Longer than wide, e.g. *Sinespinaspis*

34. Middle furrow:
    0. Commences in front of the mid-length and runs inward at a low angle, e.g. *Diacanthaspis*
    1. In form of triangular depression in anterolateral corner of the middle body, e.g. *Apianurus*
    2. Arises at antero-lateral corner of middle body and runs inward and backward, e.g. *Exallaspis*
    3. Broad, shallow, running in from antero-lateral corner of middle body, e.g. *Selenopeltis*

35. Shoulder:
    0. Large, pointed, e.g. *Diacanthaspis*
    1. Small, pointed, e.g. *Apianurus*
    2. Broad , e.g. *Sinespinaspis*

36. Posterior lobe furrow:
    0. Transverse, e.g. *Primaspis*

1. Pointed, e.g. *Apianurus*

Thorax

37. Number of thoracic segments (Ramsköld 1991b, ch. 14):
    0. Nine, e.g. the odontopleurines
    1. Ten

38. Differentation of thoracic segments (Ramsköld 1991b, ch. 15):
    0. Strong differentation, maximum length reached at segment four (give or take one segment)
    1. Little or no differentation, at least in posterior part of thorax
    2. *Diacanthaspis* condition

39. Disposition of posterior pleural spines in thorax (Ramsköld 1991b, ch. 16):
    0. Radiating
    1. All directed subparallel posteriorly

40. Deep posterolateral furrows on thoracic axial rings defining posterior band:
    0. Present
    1. Absent

41. Horizontal pleurae of thorax:
    0. Divided by pleural furrow
    1. Unfurrowed, e.g. *Apianurus* and *Ceratocephala*
    2. Ridge on pleurae, running in convex curve forward, that runs out into long posterior pleural spine, e.g. *Selenopeltis*

42. Pleural spines of most posterior thoracic segment:
    0. Anterior pleural spine hook-like, posterior pleural spine long and backwardly directed, e.g. *Acidaspis*
    1. Anterior pleural spine hook-like, posterior pleural spine long, backwardly directed with associated small spines, e.g. *Calipernurus*
    2. Both laterally directed, no barbs e.g. *Odontopleura ovata*

3. Anterior pleural spine laterally directed with small spines, posterior pleural spine long and backwardly directed with no associated spines, e.g. *Isoprusia* and *Whittingtonia*
4. Anterior pleural spine downwardly directed (not visible in dorsal view), posterior pleural spine backwardly directed, both with associated spines, e.g. *Ceratocephala*
5. Anterior pleural spine laterally directed with small spines, posterior pleural spine long and backwardly directed, slim additional pleural spine between anterior and posterior, i.e. *Miraspis mira*
6. Anterior pleural spine laterally directly, posterior pleural spine long and backwardly directly, small spine projects from proximal end of latter, e.g. *Dalaspis*

43. Antero-lateral part of the axial ring of thorax:
    0. Not inflated
    1. Inflated, e.g. *Selenopeltis*, *Miraspis* and *Proceratocephala*

44. Inflation of the posterior pleural band of thoracic segment:
    0. Absent
    1. Present, e.g. *Primaspis*, *Leonaspis* and *Acidaspis*

45. Two nodes on axial ring of thorax:
    0. Absent
    1. Present

Pygidium

46. 'True' major border spines of pygidium (Ramsköld 1991b, ch. 21):
    0. Present
    1. Absent (present on tenth thoracic segment)

47. True major border spines 'supramarginal', i.e. genal spine base inside the pygidial border (Ramsköld 1991b, ch. 22):
    0. Yes

1. No

48. Axial furrow along first axial ring (Ramsköld 1991a, ch. 9):
    0. Distinct
    1. Weak, ring confluent with pleural ridges, e.g. *Koneprusia subterarmata* adults (earlier stages may not display this state, see lectotype: see Bruton 1966b (Ormiston 1969))

49. Posterior border (Ramsköld 1991a, ch. 15):
    0. Absent
    1. Present abaxially to pleural ridge

50. Median border spine (Ramsköld 1991a, ch. 16):
    0. Shorter than axis (may only be a node)
    1. As long as, or longer than, the axis
    2. Absent

51. Number of pairs of exterior pygidial border spines (occur laterally to major border spines, those that run from the pleural ribs derived from the first axial ring; Adrain & Chatterton 1990, ch. 17):
    0. 1 pair
    1. 2 pairs
    2. 3 pairs
    3. 4 pairs, e.g. *Koneprusia*
    4. 6 pairs, e.g. *Boedaspis*
    5. 11 pairs, e.g. *Isoprusia*
    6. None

52. Number of interior pygidial border spines (those that occur between the major border spines; Adrain & Chatterton 1990, ch. 18):
    0. 1 pair
    1. 2 pairs
    2. 3 pairs
    3. >4 pairs

4. None

53. Maximum width pygidium/sagittal length of pygidium (without spines) (Adrain & Chatterton 1990, ch. 20):
    0. Less than 2.2
    1. 2.3-2.5
    2. >2.5

54. Pygidial outline:
    0. Subsemicircular
    1. Subtriangular
    2. Subquadrate

55. Pleural ridge of pygidium:
    0. Present
    1. Absent

56. Two nodes on first axial ring of pygidium:
    0. Absent
    1. Present, e.g. *Ceratocephala*

57. Two nodes on second axial ring of pygidium:
    0. Absent
    1. Present, e.g. *Whittingtonia*

58. Two pairs of granules on pleural ridge:
    0. Absent
    1. Present, e.g. *Kettneraspis*

Ontogeny

59. Paired axial glabellar spines:
    0. Present
    1. Absent

60. Antero-lateral corners of the occipital ring:
    0. Highly inflated and merges into corners of fixigena: probably associated with the inflation of the posterior part of the cephalon during ontogeny e.g. *Ceratocephala* (without deepening of the axial furrows)
    1. Does not merge into cheeks

61. Occipital and posterior border furrows:
    0. Aligned
    1. Not aligned, e.g. *Ceratocephala*

62. Pygidial axial ring:
    0. Present displaying prominent spine pair, e.g. *Kettneraspis* (Chatterton 1971)
    1. Displaying tubercle pair, e.g. *Taemasaspis*
    2. Tubercle/spine pair absent

63. Border spines displaying short lateral barbs:
    0. Present, e.g. *Ceratocephala*
    1. Absent, e.g. *Kettneraspis*

4.2.3 RESULTS

Matrix optimisation found 7 most parsimonious trees with a length of 313 (CI 0.32, HI 0.68). The trees vary only slightly in topology (see below): but, as some inconsistencies concern the relationships of basal taxa (and, therefore, between deep branches), the strict consensus is fairly unresolved. The strict consensus tree shows the following relationships:

- the Acidaspidinae group together (clade A), derived from a paraphyletic clade containing odontopleuridines (clades B & C; this clade is paraphyletic but is preserved to avoid taxonomic violence to previous work);
- a monophyletic Ceratocephalinae (clade D); and
- a basal clade of some selenopeltines (clade E; Figure 4.1).

Uncertainties in tree topology concern:

- the relationships between *Edgecombaspis*, *Kettneraspis*, *Leonaspis* and *Laethoprusia* (trees 1, 2, 5 and 6 all display various groupings; Figure 4.2 (a));
- Trees 3, 4 and 7 display a clade common to all three (a variation of clade 3 from Figure 4.3) and associated groupings of the clade *Edgecombeaspis*, *Kettneraspis* and *Leonaspis* (Figure 4.2 (b)).
- The relationships between the basal taxa of the tree vary (Figure 4.2 (c)).

Description and analysis of the phylogeny are based on the majority-rule tree (which is almost fully-resolved (Figure 4.3)). Character states with ambiguous optimisation are indicated by asterisks next to the character in question, within the *Systematic Palaeontology* (section 4.5).

Despite a large number of resolved nodes (25 out of 43), indices of consistency and retention were quite low: CI=0.32, RI=0.51, RC=0.16. Such values indicate high levels of homoplasy in the data (343 out of 373 apomorphies were homoplastic).

4.2.4 DISCUSSION

Characters that have phylogenetic importance (i.e. those with states that have a CI of 1.0) are:

- Glabella topology around spine pair three (ch. 3);
- Presence/absence of occipital organ (ch. 9);
- Shape of hypostomal shoulder (ch. 35);
- Presence/absence of paired axial glabellar spines in ontogeny (ch. 59);
- Occipital and posterior border furrow alignment during ontogeny (ch. 61);
- Presence/absence of node/spine on pygidial axial ring during ontogeny (ch. 62); and
- Presence/absence of border spines with lateral barbs during ontogeny (ch. 63).

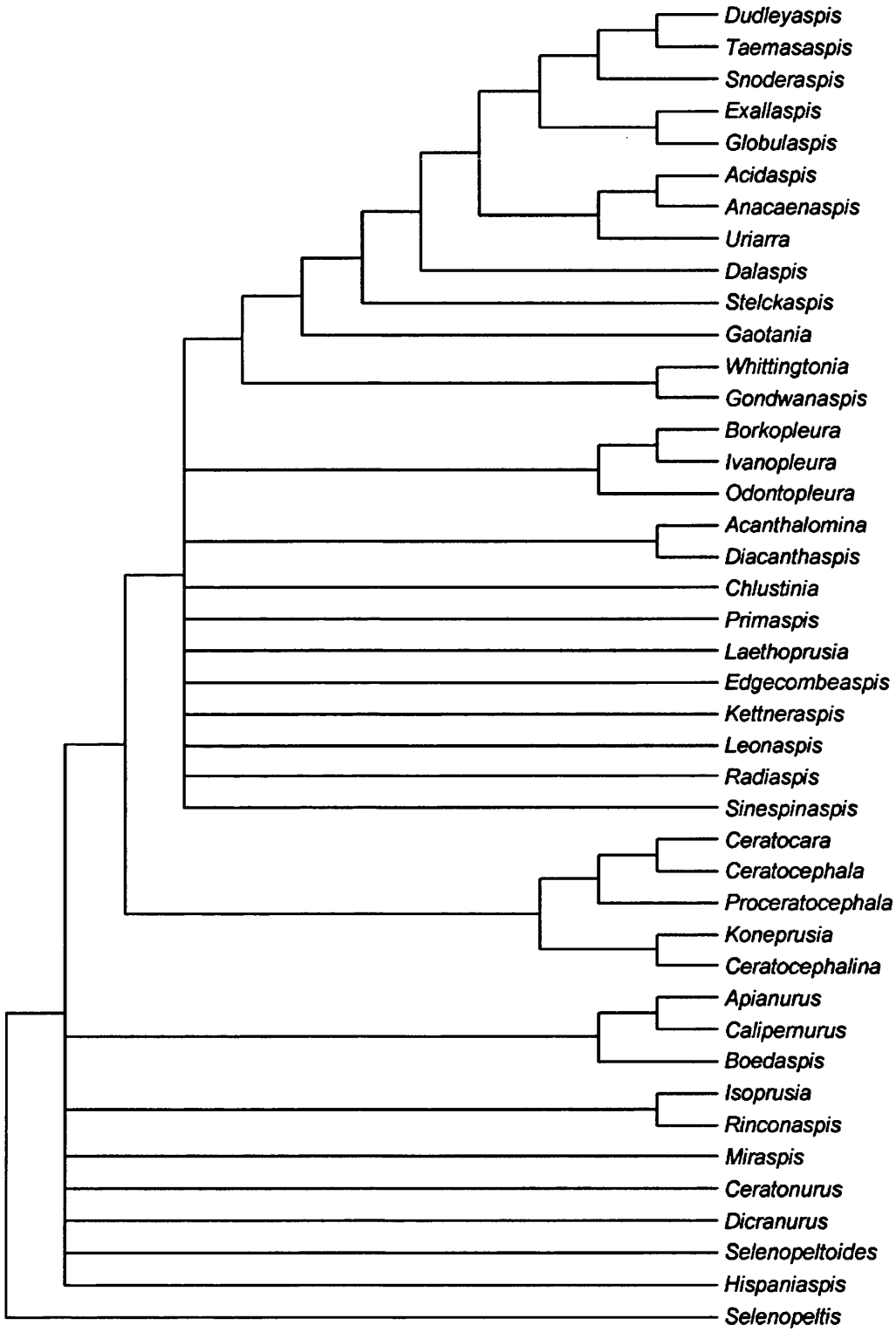

Figure 4.1: Strict-consensus tree.

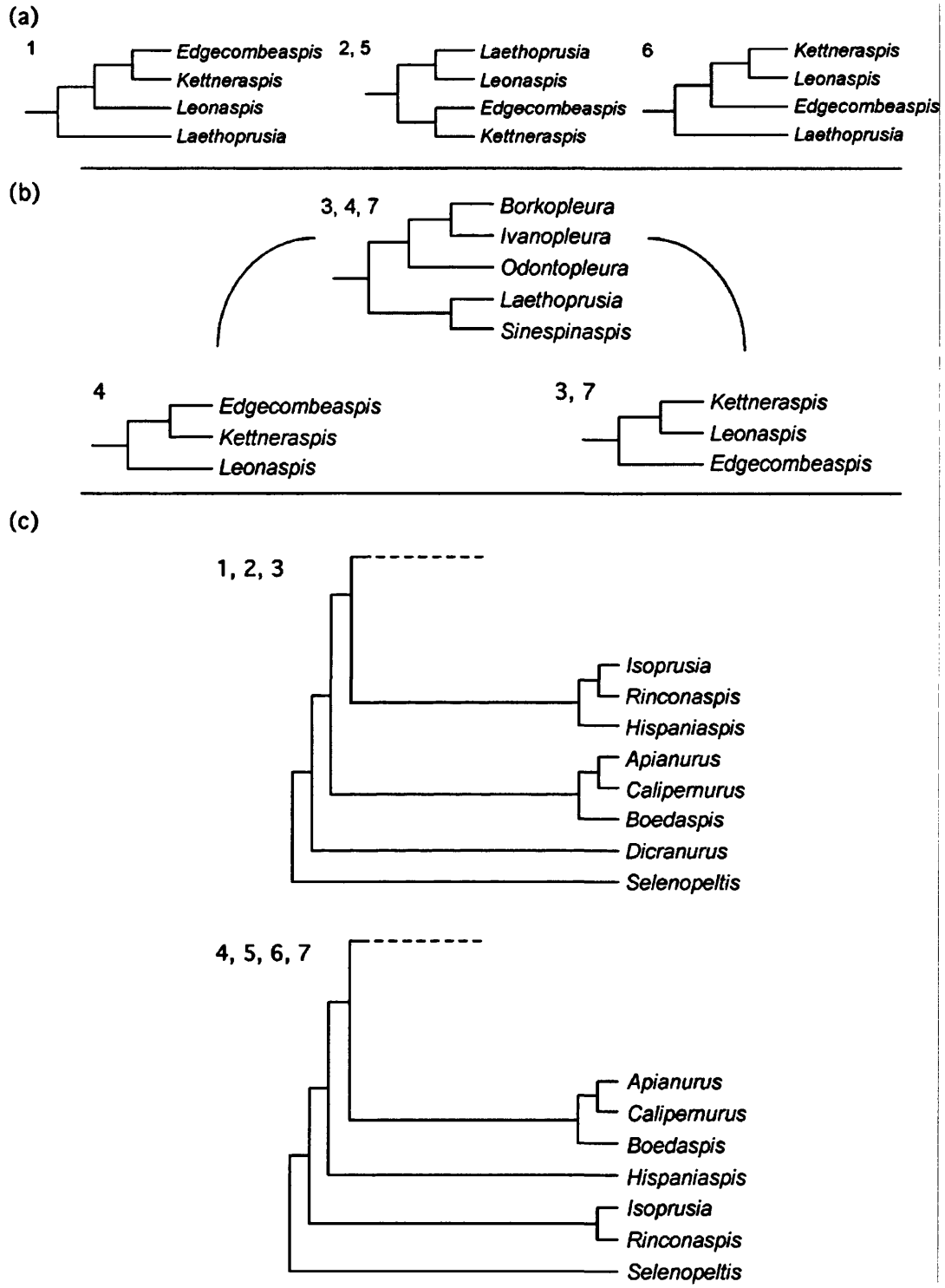

Figure 4.2: Differences between the seven resulting MPTs. The tree number is written to the left of the relationship displayed.

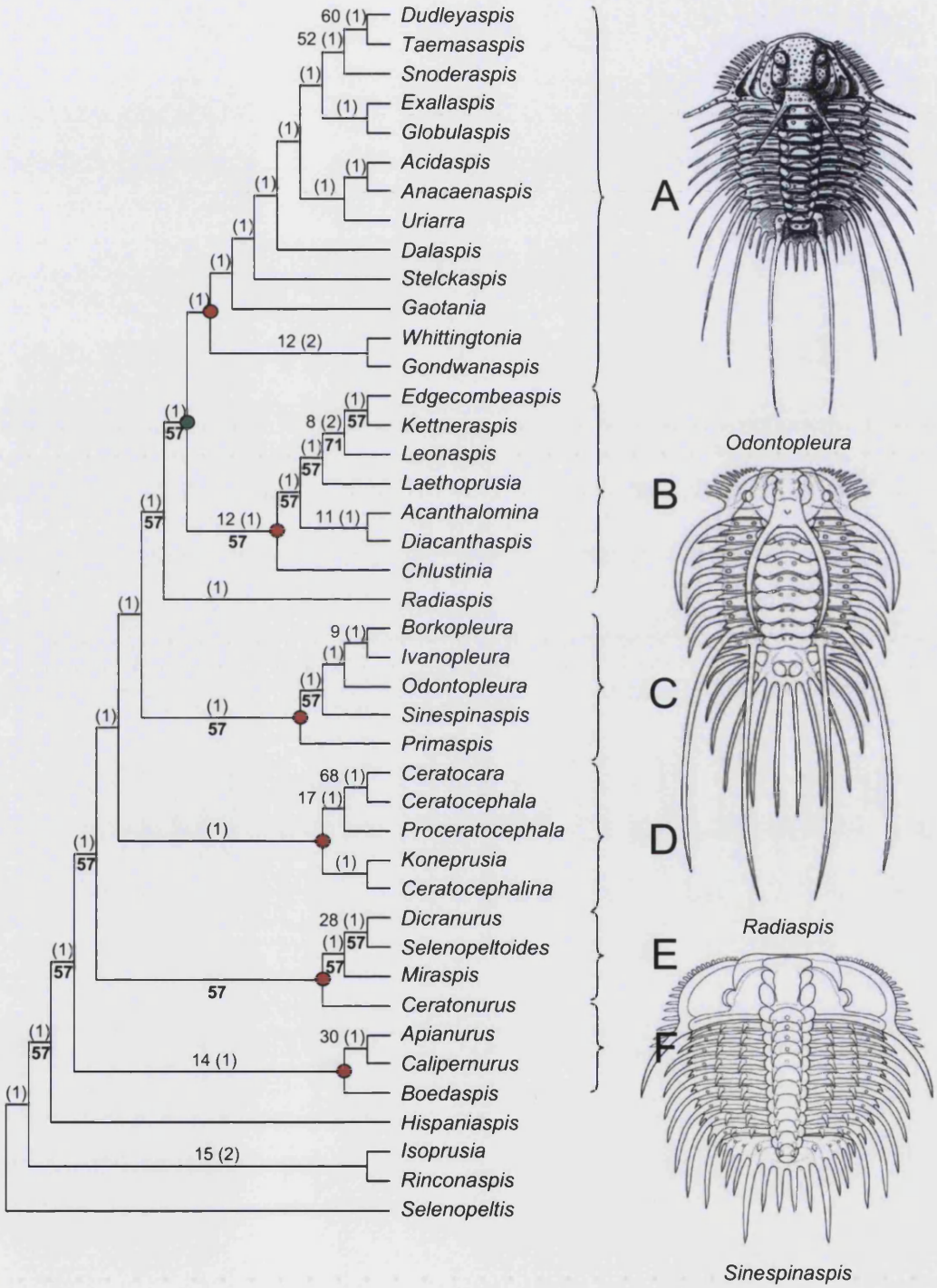
60 (1)
Dudleyaspis
52 (1)
Taemasaspis
(1)
Snoderaspis
(1)
Exallaspis
(1)
Globulaspis
(1)
Acidaspis
(1)
Anacaenaspis
(1)
Uriarra
(1)
Dalaspis
(1)
Stelckaspis
(1)
Gaotania
12 (2)
Whittingtonia
Gondwanaspis
(1) 57
Edgecombeaspis
8 (2) 57
Kettneraspis
(1) 71
Leonaspis
(1) 57
Laethoprusia
(1) 57
Acanthalomina
12 (1) 57
11 (1)
Diacanthaspis
Chlustinia
(1)
Radiaspis
(1)
9 (1)
Borkopleura
(1)
Ivanopleura
(1) 57
Odontopleura
(1) 57
Sinespinaspis
(1)
Primaspis
(1)
68 (1)
Ceratocara
17 (1)
Ceratocephala
(1)
Proceratocephala
(1) 57
(1)
Koneprusia
Ceratocephalina
28 (1)
Dicranurus
(1) 57
Selenopeltoides
(1) 57
Miraspis
57
Ceratonurus
(1) 57
30 (1)
Apianurus
14 (1)
Calipernurus
Boedaspis
(1)
Hispaniaspis
15 (2)
Isoprusia
Rinconaspis
Selenopeltis
A
Odontopleura
B
C
D
Radiaspis
E
F
Sinespinaspis

Figure 4.3: Majority-rule tree. A low cut-off limit was applied to the bootstrap values figured. Although it is acknowledged that often a bootstrap value of <50% is considered poor support for a node, it was felt important to convey the difference in support between the bootstrap support for other groupings. Bootstrap values and branch support values (given in adjacent brackets where >0) are shown above the branches. The percentage of trees that each group is retained in (where <100%) is shown below the respective branches. Clades A–F are indicated. Green nodes delineate familial groupings, red nodes delineate subfamilial. (Line drawings taken from www.trilobites.com: their positioning in the figure does not relate directly to the clade they are in).

4.3 DISPARITY

The term *disparity* is used to express morphological diversity and variety within body plans (i.e. range of morphologies) as opposed to taxonomic diversity, or the number of species. Some uses of this information are: (1) to recognize evolutionary radiations; (2) to assess extinction selectivity; (3) to evaluate morphological responses to environmental or ecological factors (e.g. Wills 1998a) and (4) to test macroevolutionary hypotheses (see Villier & Eble 2004).

Measurements of disparity among extinct arthropods have contributed greatly to our understanding of the Cambrian explosion (e.g. Leiberman 1999). Indeed, in several cases, arthropods alone have served as a proxy for entire faunas (e.g. Briggs *et al.* 1992a, b; Foote & Gould 1992; Gould 1991, 1993; Wills *et al.* 1994).

The interpretation of disparity patterns of Phanerozoic-ranging arthropods is contentious. Several workers have claimed that the Burgess Shale fauna alone (assuming this to be typical for all Cambrian faunas) contains at least twenty distinct arthropod taxa of class status or higher (e.g. Foote & Gould 1992; Gould 1989, 1993; Lee 1992). Others consider there to be little significant difference between the disparity of Cambrian and Recent faunas (e.g. Briggs *et al.* 1992a, b; Wills *et al.* 1994). The inflation of Cambrian disparity recognized by Gould (1989) was explained as an artefact of fossil *problematica* (i.e. Cambrian taxa that do not fit straightforwardly into any of the four recognized modern higher-arthropod groups being given an undeservedly-high taxonomic rank: see Waggoner 1996 for detailed discussion).

4.3.1 METHODS

4.3.1.1 Taxon and character sampling

It is often assumed that the highest quality results can only be obtained with analyses of species (see Smith & Lieberman 1999). However, some studies suggest that sampling at specific- and generic-levels provide equivalent estimates of the global disparity signal (Foote 1995, 1999). Many disparity studies, therefore, focus on genera (e.g. Raup & Boyajian 1988; Villier & Eble 2004), as is commonly done with taxonomic diversity data.

However, two very significant assumptions are made when sampling genera: (1) that the differences between species of separate genera exceed differences between species within genera; and (2) that, on average, the morphology of a sampled species can be taken as representative of the morphology of its genus (see Villier & Eble 2004).

Each genus was exemplified by one species in this study, which was then treated as representative of the genus throughout its stratigraphic range.

Variable morphology between species within genera was coded into the primary dataset to be used in the phylogenetic analysis (some taxa contain species with two or more specific states). The multivariate methods used to quantify disparity, however, cannot incorporate uncertainties or multiple codings and this information was re-coded to be applicable (see section 4.3.1.3)).

Of course, the choice of characters is a fundamental and significant aspect of disparity studies, just as it is in phylogenetics. They must cover a wide range of morphological features, coded from characters that are likely to be well-preserved and cover each taxon globally (see Roy & Foote 1997).

4.3.1.2 Temporal sampling

GeoWhen (http://www.stratigraphy.org/geowhen; accessed summer 2005) was used to gather information on absolute temporal scales: time was resolved to geological stage (see Figure 4.4). Where few taxa (<2) share the same stage, the latter were amalgamated into larger temporal intervals (G1-G6; see Appendix V). These time intervals were defined to minimize variation of their average duration and to maximize the reliability of the stratigraphic ranges, whilst still remaining useful for examining macroevolutionary patterns.

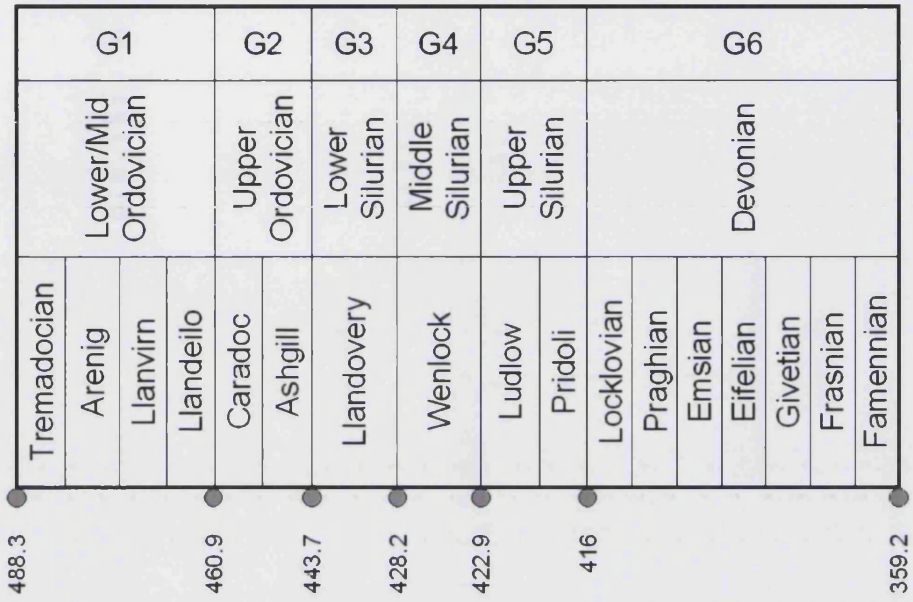

Figure 4.4: Temporal scale used in this study. Values indicate age of stage boundaries in Myr (from http://www.stratigraphy.org/geowhen/geolist.html). Intervals made of amalgamated stages used here (G1-G6) are shown on the top and geological stage in the centre.

Odontopleurids have been extensively studied and the stratigraphic ranges of most genera are reliable at the stage level. Stages seem to be the shortest operational time interval for Odontopleuroidea as a whole. Uncertainty and risk of erroneous stratigraphic attribution increase at finer resolution but sampling at the stage level would improve stratigraphic resolution.

4.3.1.3 Euclidean distance analyses and Principal Coordinates Analysis (PCA)

Landmark and distance measurement methods were discarded in favour of disparity inferred from discrete characters. As phylogenetic analysis was also intended, the same dataset was used.

The volume of *morphospace* occupied by any group provides a proxy for its disparity. Univariate ranges or variances can be added or multiplied to obtain a single, multivariate index of the amount of 'morphospace' occupied (see Wills *et al.* 1994). Those clades that display high disparity will, therefore, occupy a large morphospace: and *vice versa*.

Euclidean distance analysis: The first analysis conducted was a Euclidean distance analysis on the raw dataset (Appendix IV) calculating the mean distance between all genera from a given time interval using MATRIX (Wills 1998b). No differential weighing among characters was assumed. Essentially, this test determines dissimilarity metrics between taxa, with like forms plotting more closely together than unlike. The more unique a taxon, the further away it falls from other taxa. This distance matrix summarizes what is considered to be the phenetic information (or *numerical taxonomic* information).

Phenetics is a school of taxonomy that classifies organisms on the basis of overall morphology: it involves observable similarities/differences irrespective of whether or not the organisms are related. No attempt is made to distinguish between plesiomorphic and derived characters: unlike cladistics, which uses character polarity. The matrix usually takes a complement for metrics scaled between 0.0 (where the compared states match) and 1.0 (where the compared states do not match). This expresses how phenetically proximate or distant each taxon is in relation to every other taxon assessed, in a numerical fashion.

Not all character states could be coded as they were not well-preserved. These missing entries affect how the data can be treated. Deleting all traits not coded by all characters would have eliminated a vast amount of the available data. Most programs that perform standard PCA (see below) will not accept missing data statements in a dataset.

The general approach advocated here for binary (two state) and ordered multistate (more than two states) characters is to replace missing data with the mean value for each character (sum of codes of all character states divided by the number of

taxa coded for that character). This means that a taxon coded as '?' for a given character will be placed at the centre of gravity for the character as a whole. The variance of the character will be very slightly reduced, but only in proportion to the number of originally uncoded taxa. As an extreme and hypothetical example, a taxon with all characters missing would be placed at the global centroid and located at coordinate 0.00 on each PC axis. A simple example of the coding of one simple binary and one ordered multistate character is the following:

	Character	
Taxon	A (binary)	B (ordered)
A	0	2
B	1	3
C	0	1
D	?	0
E	?	?

gives:

	Character	
Taxon	A (binary)	B (ordered)
A	0	2
B	1	3
C	0	1
D	0.33 (1/3)	0
E	0.33 (1/3)	1.5 (6/4)

Unordered, multistate characters can be incorporated into PCA by rescaling a non-additive binary representation. Such characters may also be scored with missing data for certain taxa, and a procedure is needed for placing such points at the centre of gravity for the overall character-state distribution. This may be achieved in a manner analogous to that for binary or ordered characters. The first step is to recode the unordered character into non-additive binary, propagating missing values into all the binary columns.

For example:

Taxon	Character A (unordered)
A	0
B	0
C	1
D	2
E	?

gives:

	Character		
Taxon	A (state 0)	A (state 1)	A (state 2)
A	1	0	0
B	1	0	0
C	0	1	0
D	0	0	1
E	?	?	?

Missing values are then replaced by their column means, similar to the treatment of binary characters:

	Character		
Taxon	A (state 0)	A (state 1)	A (state 2)
A	1	0	0
B	1	0	0
C	0	1	0
D	0	0	1
E	0.5 (2/4)	0.25 (1/4)	0.25 (1/4)

All columns are then rescaled by multiplying by 0.707 (reciprocal of $\sqrt{2}$) – in order to bring all interstate distances equal to one unit:

	Character		
Taxon	A (state 0)	A (state 1)	A (state 2)
A	0.707	0	0
B	0.707	0	0
C	0	0.707	0
D	0	0	0.707
E	0.354	0.177	0.177

When this last matrix is ordinated onto PC axes, taxa (A+B), C and D are related in an equilateral triangle (with all intertaxon distances equal to one unit) while taxon E is located at the centre of gravity for A to D, in the plane of the triangle.

The reason that columns are rescaled by 0.707, and the intertaxon distances thereby equalled to one unit, is to prevent multistate characters having increased influence on the analysis. Without rescaling, the intertaxon distance would be $\sqrt{(1^2+1^2)}$ (1.414 units); all intertaxon distances are rendered to 1 unit if the dataset is rescaled by $1/\sqrt{2}$ (0.707; see Figure 4.5).

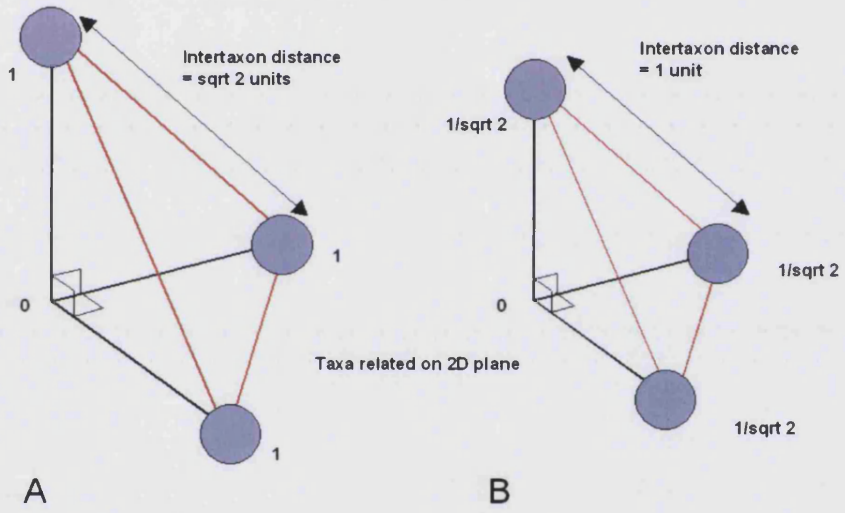

Figure 4.5: Three taxa (blue circles) each have one of the three alternative recoded states of an three-state, unordered character. The character has been broken down into three dichotomous characters (three axes) each coding '1' for a single taxon and '0' for the other two (see tables above). A. The apparent distance between all pairs of taxa will be inflated from one 'unit of character-state difference' to $\sqrt{2}$; B. the rescaling of the non-additive dichotomous columns representing a multistate character so as to render all distances to one unit (redrawn from Wills *et al.* 1994, figure 2).

Principal Coordinates Analysis (PCA): In all but the simplest cases, the structure of the eigenvalues is not easily appreciated, and some method is required to reveal it. Where the aim is taxonomic, and where a hierarchical structure is sought, some clustering algorithm is appropriate. This is achieved by a second analysis: a data reduction analysis, such as principal component analysis (PCA) or principal coordinates analysis (PCO). This is calculated by way of a multivariate statistical package, e.g. MVSP 87

(Kovach 1990). This program produces a near-Euclidean triangular distance matrices from large datasets.

The first principal component (PC or *axis*) represents those characters that contribute most to overall disparity (and is equivalent to the major axis line through the points). The second PC, orthogonal to the first, acts with the first to explain the best-fitting plane, with each additional axis added representing ever-decreasing fractions of the total variance. In the extreme situation where all characters are perfectly correlated, the PC analysis would present all variation on the first single axis.

The most common measures of dissimilarity on any given axis are *variance* and *range* (Foote 1991a). The former is most appropriate when looking at the *average* dissimilarity between forms – and is therefore less sensitive to outliers – but the range is best used when an indication of *overall* morphological variation is required. The MVSP data for these axes were read into a rarefaction program, RARE 1.1 (Wills 1998c): this was used to calculate the sums and products of both the variance and range with varying numbers of coordinate axes and allows comparison between samples of different sizes.

Rarefaction analyses operate by approximating empirically the expected morphological variation in sample sizes between 2 and the total number of taxa in the group in question (Foote 1992; Wills 1994). For each sample size, an appropriate number of taxa is pulled randomly from the group (sampling without replacement). Here, the first twenty-three principal coordinate axes (out of the 107 calculated in total) were utilized for the entire sample as these encompassed 90% of the total variance. Although, this figure of 90% is arbitrary – a cut-off point is needed – and the later components incorporate only trivial aspects of correlation individually and can be discarded. It should be remembered, however, that all the data used has contributed in some way toward the orientation of the component axes in the first place.

The morphological variety for this sample is calculated and noted and the sampled taxa replaced. The process is repeated a thousand times to give a mean value and confidence intervals. A plot of morphological variety against sample size can be used to compare the behaviour of all samples.

Statistical tests can be applied (as in the study by Stockmeyer Lofgren *et al.* 2003) but there are several problems with conducting statistical tests on these data as they assume the taxa are independently distributed in morphospace. This assumption is violated because all trilobites share common ancestry (phylogenetic autocorrelation;

Felsenstein 1985). Moreover, ANOVA tests on the Euclidean distance measure would give values only for the *derivedness* of groups of taxa (from the outgroup) rather than their true disparity (see Wills 1994, pp.108-109 for discussion).

4.3.2 RESULTS

4.3.2.1 Analysis by age: Euclidean distance analyses of PCA data

A basic Euclidean distance analysis was performed on the PCA results of the entire dataset – resulting in a 42-taxon dataset. Distances from the outgroup for all ages range from 4.243 (e.g. *Leonaspis*) to 5.916 (e.g. *Gaotania*). The arrangement of the organisms from the analysis can be found in Figure 4.6: the six groups appear interspersed. All taxa plot far from *Selenopeltis* as it is the outgroup and they have diverged away from this primitive morphology.

It is important to note that this test only deals with the distance from an outgroup, i.e. overall morphological differences from the outgroup, rather than overall morphospace *per se.* It gives no indication of the arrangement of the taxa in relative morphospace, i.e. two taxa located at a similar distance from the outgroup might be nearly on top of one another, or they might be endpoints of a straight line equidistant from the outgroup.

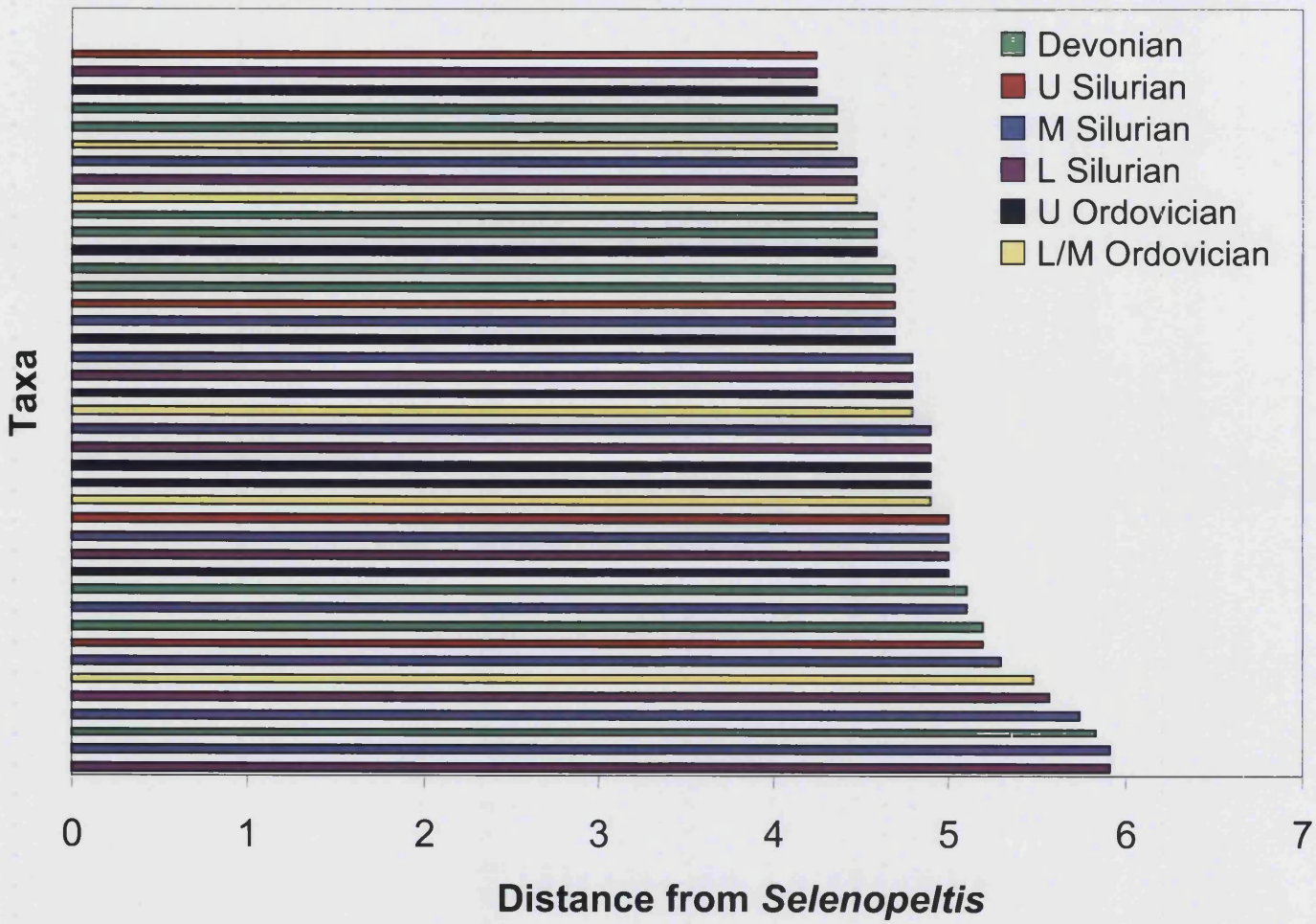

Figure 4.6: Results from Euclidean distance analysis of raw data. Each horizontal bar represents one taxon. Distance was calculated by using *Selenopeltis* as the outgroup. Taxon bars are coloured according to the time-slices specified.

4.3.2.2 Analysis by age

Taxa from all time slices seem evenly distributed and interspersed. Mean disparity of each sample shows a decreasing trend through time, with an unexpected increase before extinction in the Devonian (Figure 4.7).

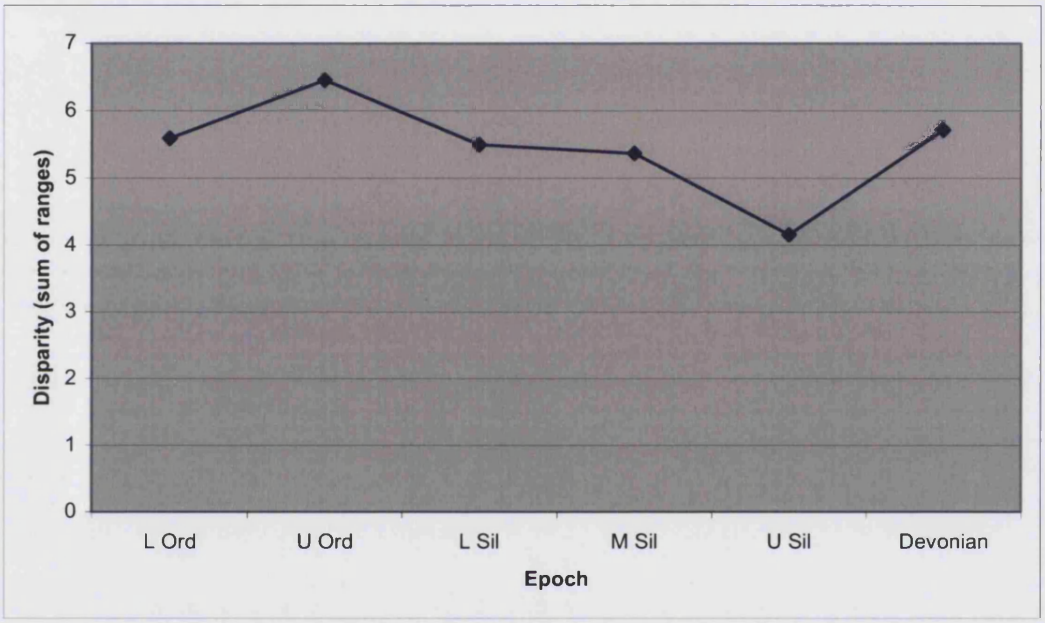

Figure 4.7: Mean disparity of odontopleurid taxa through time (i.e. plotted mean end-point of curves from 4.8).

A test was conducted on the sum of ranges data for all time slices on all coordinate axes (see Appendix VI for raw data) to see if the disparity of taxa at any given time was significantly different from random from a similar-sized sample drawn from the universe of all realized body-plans (Figure 4.8).

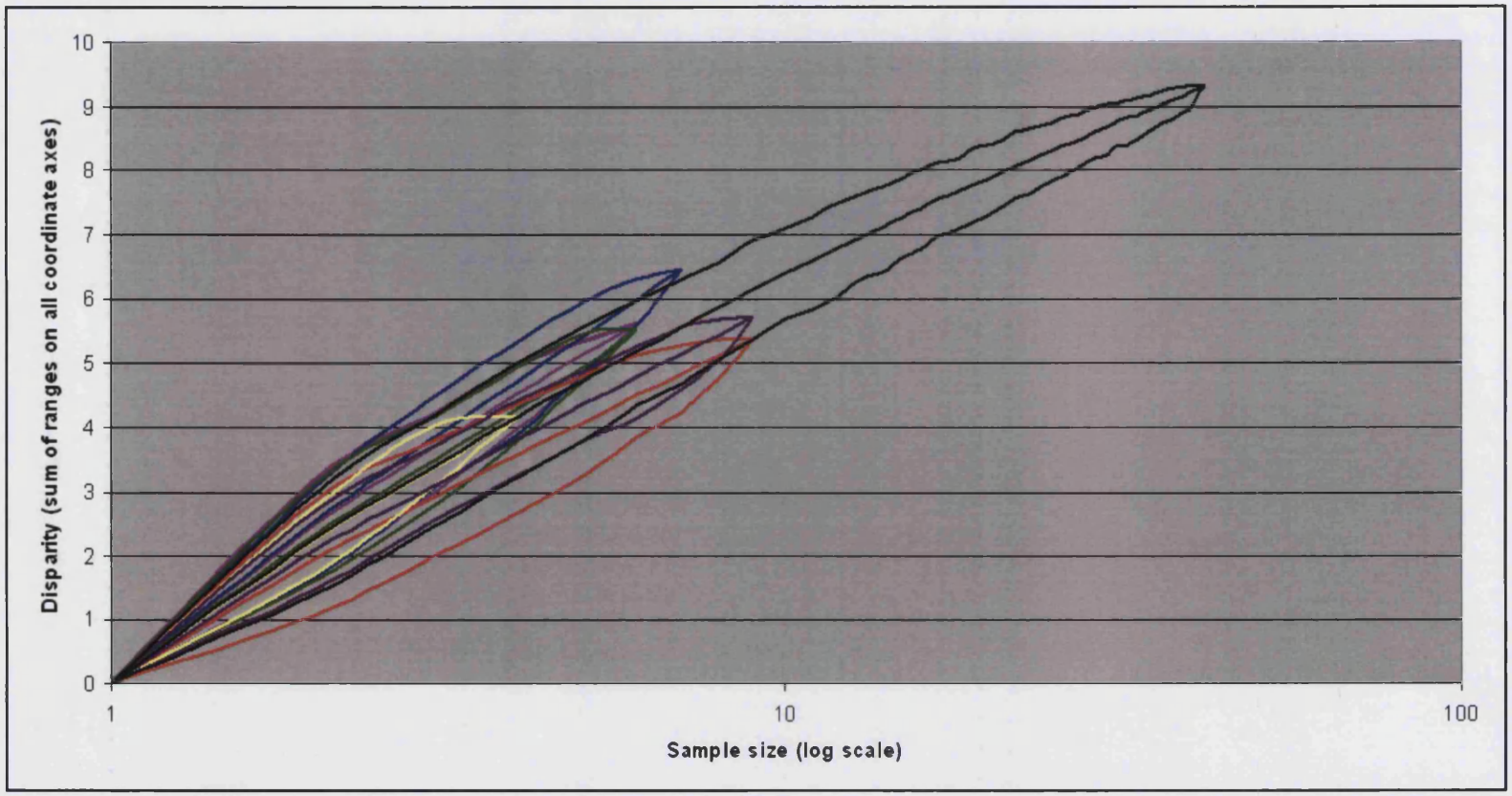

Figure 4.8: Rarefaction curves of measures of morphological disparity for taxa in different time slices compared to that of entire dataset (sum of ranges data: 1000 random draws of taxa were made by randomising at each sample size, providing a mean value for the respective measure of morphological variety, along with upper and lower 90% confidence limits). Black = all taxa; pink = Lower Ordovician taxa; blue = Upper Ordovician taxa; green = Lower Silurian taxa ; red = Middle Silurian taxa; yellow = Upper Silurian; purple = Devonian.

Values of species in time slices are not significantly different when compared to the entire dataset (all values lie within the 90% confidence limits for the whole dataset). But, although the rarefaction curves follow broadly similar trajectories, the Middle Silurian and the Devonian taxa occupy significantly less morphospace per unit of taxonomic richness than those from the Lower Ordovician, Upper Ordovician and Upper Silurian (Figure 4.8).

The Lower and Upper Ordovician taxa have significantly higher disparity to those from Middle Silurian and Devonian (their mean values lie outside the 90% confidence limits of the Middle Silurian and Devonian taxa).

4.3.2.3 Analysis by clade

The clades display differing levels of mean disparity, with Acidaspidinae and Odontopleurinae having higher mean disparity than other odontopleurid clades (Figure 4.9).

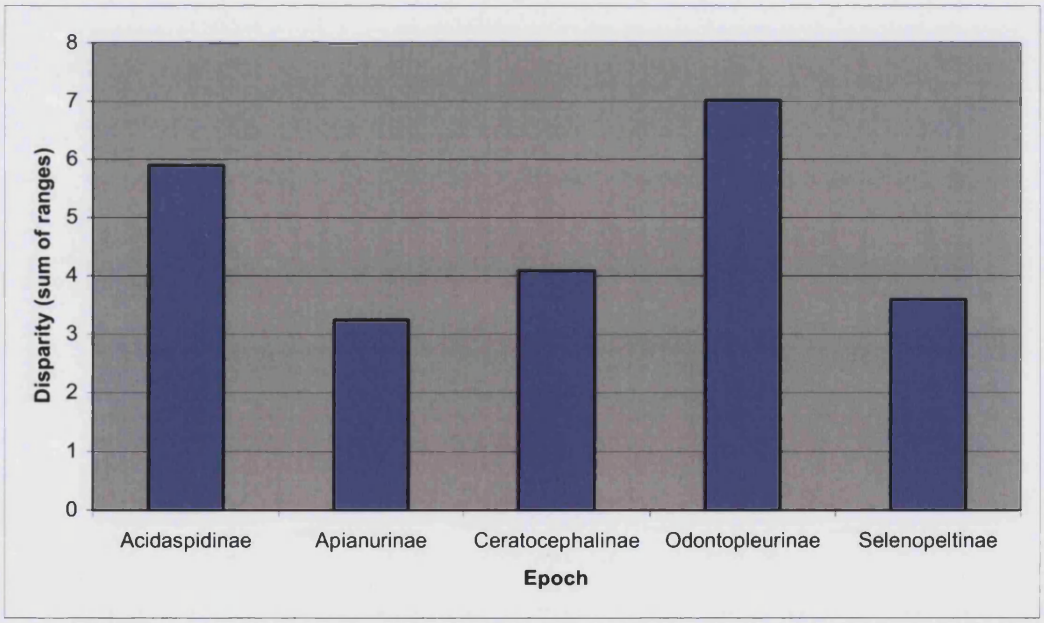

Figure 4.9: Mean disparity of clades of odontopleurid taxa as a histogram (i.e. plotted mean end-point of curves from 4.10).

A test was conducted on the sum of ranges data for all clades (see Appendix VII for raw data; Figure 4.10).

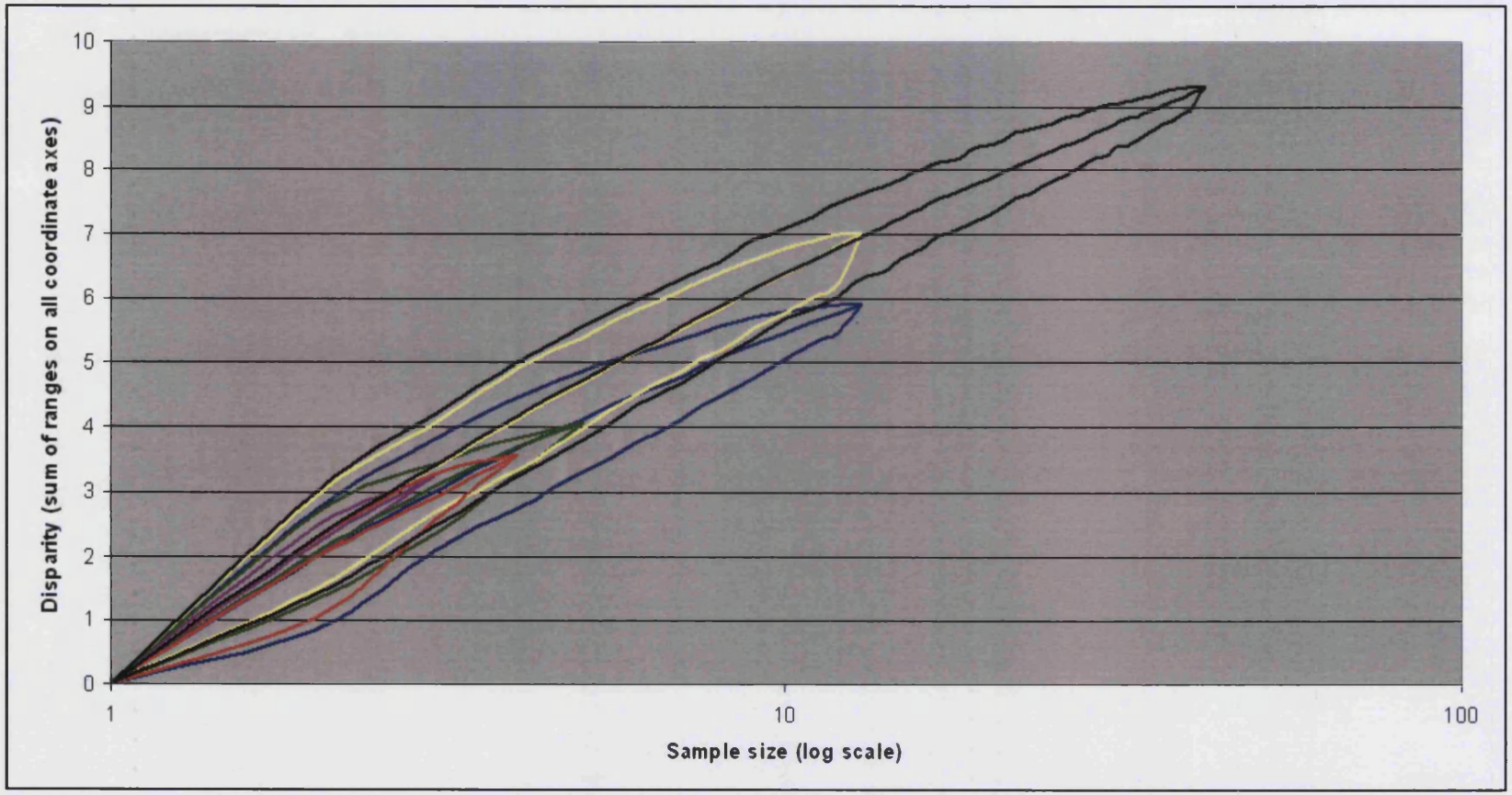

Figure 4.10: Rarefaction curves of measures of morphological disparity for different odontopleurid clades (sum of ranges data: 1000 random draws of taxa were made by randomising at each sample size, providing a mean value for the respective measure of morphological variety, along with upper and lower 90% confidence limits). Black = all taxa; pink = Apianurinae; green = Ceratocephalinae; blue = Acidaspidinae; yellow = Odontopleurinae; red = Selenopeltinae.

Disparity values of the different clades are not significantly different when compared to the entire dataset (all values lie within the 90% confidence limits for the whole dataset): all rarefaction curves follow broadly similar trajectories.

However, the Odontopleurinae has statistically-significantly higher disparity compared to the Acidaspidinae (but neither show different disparity levels to the other groups; the mean values of Acidaspidinae lie outside the 90% confidence limits of the Odontopleurinae; Figure 4.10).

4.3.2.4 Principal Coordinates Analysis (PCA)

Plotting the first few PCA/PCO axes allows the data to be viewed from the angle that maximizes the amount of overall variance represented, given that one is restricted to graphically depicting a small number of orthogonal axes (Figure 4.11). It should be stressed, however, that one is limited to presenting only a proportion of the variance in the original data, while calculations derived from a PCA/PCO can be based on all components, and therefore encompass all of this variation.

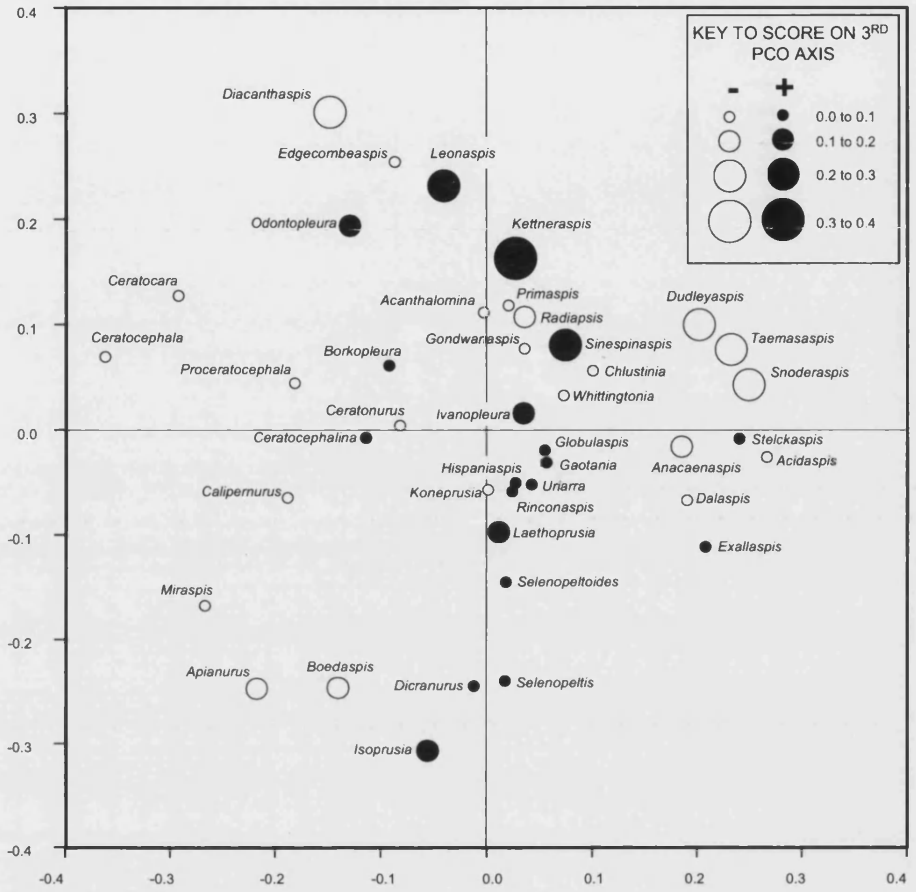

Figure 4.11: Mean disparity of odontopleurid taxa.

Analysis by age: Results for the first three PCA axes are plotted in a graph (Figure 4.12). Time slices plot in overlapping areas of morphospace defined by the first three principal coordinate axes.

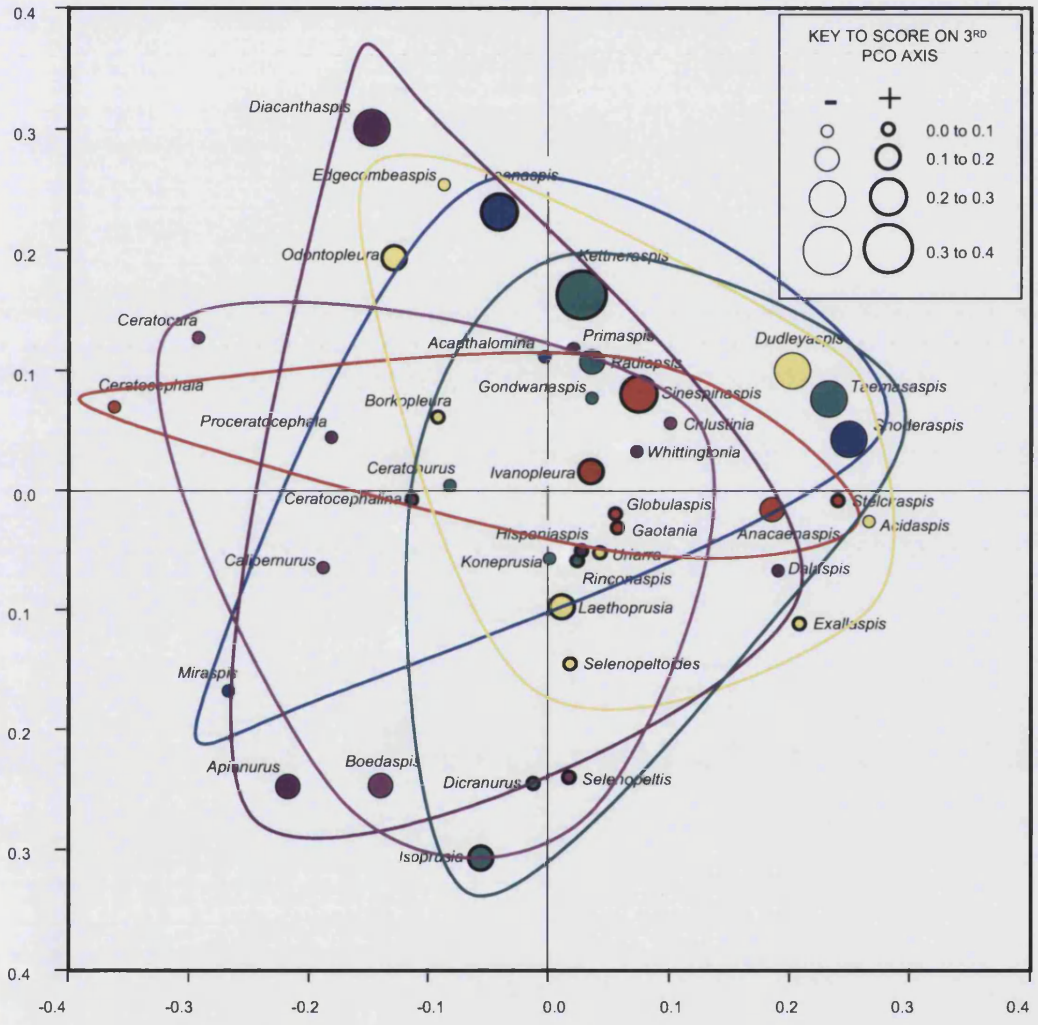

Figure 4.12: Distribution on the 1st three principal coordinates axes of all genera divided into age categories. The 1st two PCA axes are shown as the axes of the graph and the third axis is indicated by size of the circles. (Middle Ordovician = light purple; Upper Ordovician = deep purple; Lower Silurian = red; Middle Silurian = yellow; Upper Silurian = blue; Devonian = green).

Analysis by major taxonomic group: Results for the first three PCA axes are plotted in a graph (Figure 4.13). Major groups plot in distinct and generally non-overlapping areas of morphospace defined by the first three principal coordinate axes.

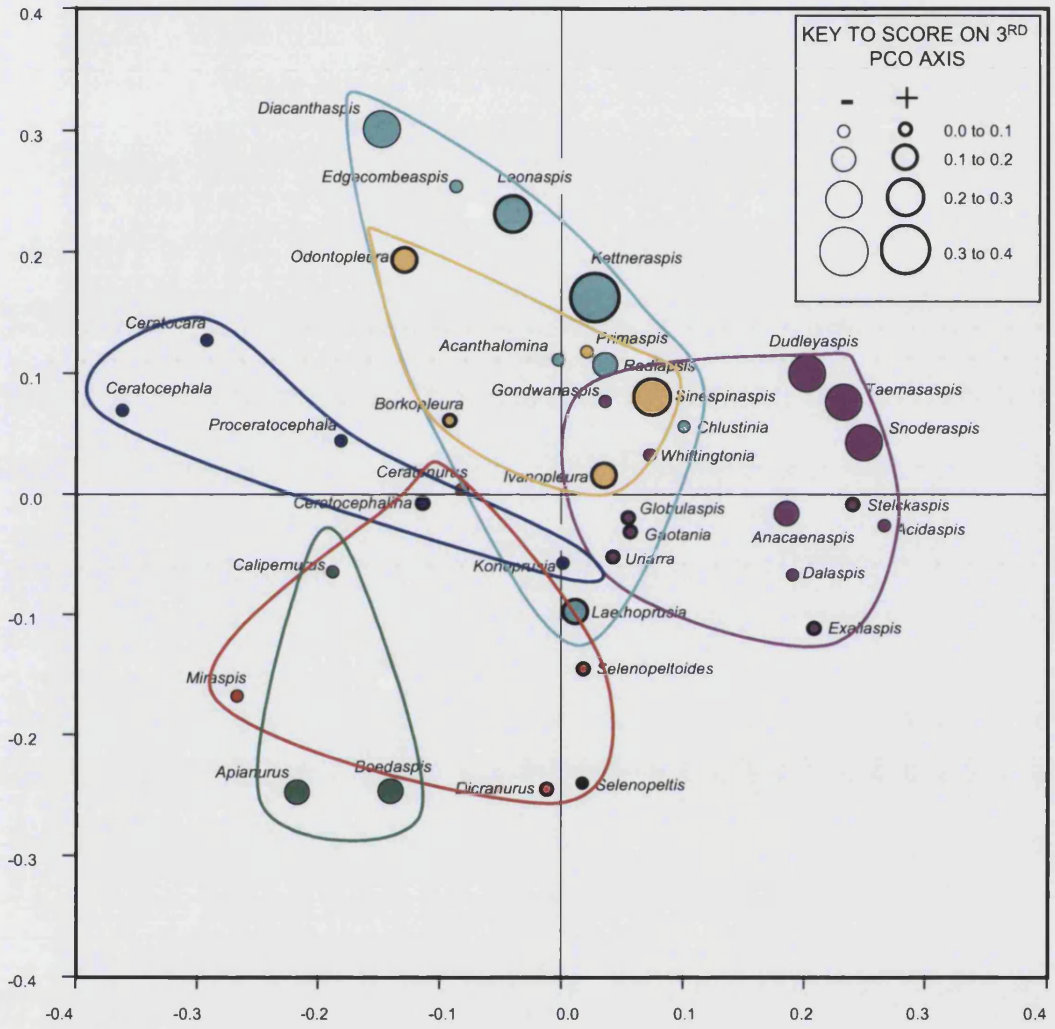

Figure 4.13: Distribution on the 1st three principal coordinates axes of all genera divided into clades. The 1st two PCA axes are shown as the axes of the graph and the third axis is indicated by size of the circles. Taxa are identified by coloured circles as to their major taxonomic grouping (clade A [Acidaspidinae] = purple; [Odontopleurinae] clade B = turquoise and clade C yellow; clade D [Ceratocephalinae] = navy blue; clade E [Selenopeltinae] = red; clade F [Apianurinae] = green).

4.4 DISCUSSION

4.4.1 PHYLOGENETIC ANALYSIS (see *Systematic Palaeontology*, section 4.5)

4.4.2 DISPARITY

4.4.2.1 *Disparity patterns over time*

The mean of the sum of ranges data from the rarefaction analysis suggests that mean disparity later in time was about equal to earlier in time (with a slight rise in the Upper Ordovician and a slump in the Upper Silurian; Figure 4.7).

However, the overall picture suggests that the Lower and Upper Ordovician taxa had significantly higher disparity to those from the Middle Silurian and Devonian (Figure 4.8). In general, then, it can be said that morphological disparity is significantly lower in the stratigraphically younger taxa than the older taxa. In other words, odontopleurid groups that originated later had significantly lower disparity than those that originated earlier. In a previous study of trilobite disparity, the Ordovician is known to be a period of high morphological diversity (see Foote 1991b).

Why would there be a decline in disparity after an initially high level? If a group fails to colonize some regions of morphospace after the initial phases of its radiation, it is tempting to speculate that further exploration is stabilized and constrained. But, if this is indeed the case, the reasons remain elusive at present. It has also been suggested that the Ordovician-Permian reduction of trilobite disparity may be correlated with the corresponding rise of the Crustacea (particularly the Eumalacostraca, which, like the trilobites, were predominantly benthic scavengers and predators; see Wills 2003).

A broad study of trilobite disparity through time showed a peak in disparity later in their history than the peak in diversity (Foote 1993; but this may be just an exaggerated result caused by excessive taxonomic-splitting of Cambrian trilobite taxa). This seems to be exceptional: other groups show exploration of morphological extremes early in their history (Wagner 1995). This study suggests that odontopleurids display a different pattern to that of overall trilobite disparity as shown by Foote: they show a peak in disparity very close to their origin.

The PCA analysis results show that the groupings are vastly overlapping. There seems to be a shift of occupied morphospace over time: a small rotation around the axes centre occurs (Figure 4.12).

4.4.2.2 *Taxonomic disparity patterns*

Although the clades display differing mean disparity values (Figure 4.9) most of these differences are not significantly different. The one exception being that the Odontopleurinae has significantly higher disparity to the Acidaspidinae (Figure 4.10).

Although not significantly different, the major clades from the resulting phylogeny do seem to occupy discrete areas of morphospace when plotted along the three first PCA axes (Figure 4.13) and some groups cluster more tightly than other groups (e.g. clade F *cf.* clade E).

4.5 SYSTEMATIC PALAEONTOLOGY

Order **ODONTOPLEURIDA** Whittington, 1959

Family **ODONTOPLEURIDAE** Burmeister, 1843

TAXA INCLUDED. Subfamilies Acidaspidinae Salter, 1864, Ceratocephalinae Richter & Richter, 1925, Selenopeltinae Hawle & Corda, 1847, Apianurinae Whittington, 1956a and 'grade' Odontopleurinae Burmeister, 1843, plus taxa *Hispaniaspis* Hammann, 1992, *Rinconaspis* Baldis & González, 1981, *Isoprusia* Bruton, 1966a and *Selenopeltis* Hawle & Corda 1847.

STRATIGRAPHICAL RANGE. Lower Ordovician to Upper Devonian.

REMARKS. The subfamily Koneprusiinae Vanêk & Pek, 1987 (i.e. *Koneprusia*, *Isoprusia* and *Laethoprusia*) is not robust. Diagnostic characters given in the work by Vanêk & Pek (1987) were either pleisomorphic or erroneous (see Ramsköld 1987, p. 133). The diagnosis given in Ramsköld (1987) was preliminary. Indeed, most of the characters given by Ramsköld apply to many other genera and the combination of those morphological traits is not enough to pull those three taxa into a group outside the Odontopleurinae. Full details of the diagnoses have never been published but some of the concepts previously generated are validated in this study, e.g. the resurrection of the Acidaspidinae Salter, 1864 by Ramsköld & Chatterton (1991) is supported.

Subfamily **ACIDASPIDINAE** Salter, 1864

EMENDED DIAGNOSIS. Occipital node with occipital organ present (ch. 9*). Absence of paired occipital spines (ch. 10*; present in *Whittingtonia*). Granular ornament (ch. 21; large tubercles in more derived taxa). Absence of a functioning facial suture in holaspis (ch.25; reversed in *Exallaspis* and *Globulaspis*). Tiny border spines of librigena (ch. 27; elongate in *Snoderaspis*, *Dudleyaspis* and *Taemasaspis*). Ten thoracic segments (ch. 37). Little/no differentation of thoracic segments (ch. 38*). Posterior pleural thoracic spines all directed subparallel posteriorly (ch. 39; but they are radiating in *Acidaspis* and *Anacaenaspis*). Deep posterolateral furrows defining posterior band (ch. 40; absent in *Exallaspis*). Paired axial glabellar spines absent in ontogeny (ch. 59*; where known). Tubercle pair on pygidial axial ring in ontogeny (ch. 62*; where known). Border spines absent in ontogeny (ch. 63*).

TAXA INCLUDED. *Acidaspis* Murchison, 1839; *Anacaenaspis* Bruton, 1967; *Dalaspis* Chatterton & Perry, 1983; *Dudleyaspis* Prantl & Přibyl, 1949; *Exallaspis* Ramsköld & Chatterton, 1991; *Gaotania* Zhang, 1974; *Globulaspis* Reed, 1931; *Gondwanaspis* Feist, 2002; *Snoderaspis* Ramsköld, 1984; *Stelckaspis* Chatterton & Perry, 1983; *Uriarra* Chatterton & Campbell, 1980; *Whittingtonia* Prantl & Přibyl, 1949.

STRATIGRAPHICAL RANGE. Upper Ordovician (Medinan) to Upper Devonian (Frasnian).

REMARKS. *Taemasaspis* proves to be very-closely related to *Dudleyaspis*, as suggested by Chatterton (1981), Thomas (1981) and Ramsköld (1984). It is reasonable to assume these genera are synonymous: they are identical for all characters that it was possible to code. More specifically, *Taemasaspis* should be thought of as being a junior synonym of *Dudleyaspis.*

Snoderaspis is also closely related to *Dudleyaspis* but differs in the following characters. It has: weakly defined occipital lobes (ch. 16); anterior margin curved into three lobes (ch.20); pleural spines of thoracic segments are laterally directed (ch. 42); absence of 2 nodes on first and second axial pygidial rings (chs 56 and 57).

The relationship between *Anacaenaspis*, *Acidaspis* and *Dalaspis* has been the subject of debate and a formal phylogenetic analysis was needed (Chatterton & Ludvigsen 2004). This study identifies that *Anacaenaspis* and *Acidaspis* are sister-groups and closely-related to *Dalaspis. Anacaenaspis* differs from *Acidaspis* in not having the entire posterior margin of the occipital ring produced backwards as a stout median spine and does not have a posterior sutural ridge (see Bruton 1967, p. 235). *Dalaspis* is closely-related to *Acidaspis* (Chatterton & Perry 1983, p. 15) but is not thought to be synonymous here: it is separated phylogenetically by *Uriarra* and *Anaceanaspis. Uriarra* is not thought to be closely-related to *Primaspis* and *Leonaspis* here (*cf.* Chatterton & Campbell 1980, p.98) but is similar to *Gaotonia* (as suggested, *ibid*).

Small growth stages of *Stelckaspis* are similar to *Acidaspis* and *Dudleyaspis* (Chatterton & Perry 1983, p. 15) and here those taxa are shown to be fairly closely-related. The monophyletic '*Stelckaspis* group' (as defined by Ramsköld & Chatterton (1991; although no apomorphies were given): *Stelckaspis*, *Gaotania*, *Globulaspis* and *Uriarra*) is not monophyletic in the present analysis. Rather, *Stelckaspis*, *Gaotania* and *Uriarra* are closely-related and *Globulaspis* is closely-related to *Exallaspis. Globulaspis*

and *Exallaspis* both have a functioning facial suture (ch. 25; *cf. Gaotania* and *Stelckaspis*).

Whittingtonia is proved to be an acidaspidine rather than an odontopleuridine (see Ramsköld & Chatterton, 1991, p. 362 for discussion on contention). *Gondwanaspis* appears sister-group to *Whittingtonia* rather than to *Dudleyaspis* (*cf.* Feist 2002).

Globulaspis is closely-related to *Acidaspis* (as suggested by Reed 1931) and *Acanthalomina* and *Diacanthaspis* are also. The latter pair may be synonymous as suggested by Chatterton & Perry (1979) but *Acanthalomina* differs in the following ways: regular rows of tubercles on anterior border rather than irregular (ch. 2); tubercles on fixigena same size (ch. 5); absent O_{ap} spines rather than posterior to median occipital node (ch. 12); low eye rather than elevated (ch. 13); strong differentation within the thorax (ch. 38); two nodes on 2nd axial ring of pygidium present (ch. 57).

'Grade' **ODONTOPLEURINAE** Burmeister, 1843

TAXA INCLUDED. *Acanthalomina* Prantl & Přibyl, 1949; *Borkopleura* Šnajdr, 1984a; *Chlustinia* Přibyl & Vaněk, 1965; *Diacanthaspis* Whittington, 1941; *Edgecombeaspis* Adrain & Ramsköld, 1997; *Ivanopleura* Šnajdr, 1984a; *Kettneraspis* Prantl & Přibyl, 1949; *Laethoprusia* Ramsköld, 1991a; *Leonaspis* Richter & Richter, 1917; *Odontopleura* Emmrich, 1839; *Primaspis* Richter & Richter, 1917; *Radiaspis* Richter & Richter, 1917; *Sinespinaspis* Adrain & Chatterton 1990.

STRATIGRAPHICAL RANGE. Middle Ordovician to Middle Devonian (Eifelian).

REMARKS. This taxon is explicitly paraphyletic. Clade B shares the following characteristics with taxa in clade A: (1) paired occipital spine (ch. 10); (2) anterior facial suture is parallel to axis (ch. 26) and (3) 12-13 border spines (ch. 29).

Clades B and C both share the following characteristics with taxa in clade A: (1) anterior part of L1 is the widest point of glabella (ch. 23); (2) posterior sutural ridge along posterior facial suture (ch. 32) and (3) two nodes on the 2nd axial pygidial ring (ch.57).

It shows the following characteristics:

- *Leonaspis* has descended from *Diacanthaspis* (as supported by Chatterton & Perry 1974, p.15).
- *Radiaspis* is closely-related to *Diacanthaspis* and *Acanthalomina* (Ramsköld & Chatterton 1991, p.335).

- The Odontopleurinae as defined by Ramsköld & Chatterton 1991 is similar to the result obtained here: the study suggests the inclusion of *Chlustinia*, *Edgecombeaspis*, *Laethoprusia*, *Primaspis* and *Sinaspinaspis.*
- *Chlustinia* is shown here to have affinity with the odontopleurines rather than the acidaspines (*cf.* Ramsköld & Chatterton 1991).
- *Ivanopleura* and *Borkopleura* are closely-related to Odontopleura (as suggested by Šnajdr 1984a).

Subfamily **CERATOCEPHALINAE** Richter & Richter, 1925

EMENDED DIAGNOSIS. Wide, granulated anterior cranidial border (ch.1). Large, flattened tubercles on glabella (ch. 21*; unknown in *Ceratocephalina* and *Koneprusia*). Median border spine on pygidium that is longer than the axis (ch. 50). Occipital and posterior border furrows are not aligned in ontogenetic stages (ch. 61).

TAXA INCLUDED. *Ceratocara* Ramsköld, 1991b; *Ceratocephala* Warder, 1838; *Ceratocephalina* Whittington, 1956; *Koneprusia* Prantl & Přibyl, 1949; *Proceratocephala* Prantl & Přibyl, 1949.

STRATIGRAPHICAL RANGE. Lower Ordovician (Caradoc) to Middle Devonian (Eifelian).

REMARKS. *Ceratocara* and *Ceratocephala* are sister-taxa: this result is not unexpected: they have been thought to be synonymous previously (see Ramsköld 1991b). They share: (1) occipital spine pairs are curved outwards distally (ch. 18); (2) unfurrowed thoracic pleurae (ch. 41) and (3) no 'true' major border spines on pygidium (ch. 46). *Ceratocera* displays character states that separate it from *Ceratocephala* are: (1) A1, A2, A3 tubercles are larger than other cranidial tubercles; (2) absent posterior band on occipital ring; (3) narrow fixigena; (4) deep antennular notch; (5) parallel anterior facial suture; and (6) >16 border spines on cranidium rather than 12-13. *Proceratocephala* shares a posterior border furrow merges with palpebral furrow with a strong sutural ridge (ch. 7) and slim thorn-like spines plus small tubercles (ch. 21).

Subfamily **MIRASPINAE** Pollitt *et al.*, 2006

EMENDED DIAGNOSIS. Weakly defined occipital lobes (ch. 16). Occipital furrow is shallow medially (ch. 17). Glabella is widest at anterior part of L1 (ch. 23). Genal spines not vertically downwards-directly (ch.28). Deep posterolateral furrows defining posterior

band on thoracic axial rings (ch. 40). Antero-lateral part of the axial ring is inflated (ch. 43).

TAXA INCLUDED. *Ceratonurus* Novák, 1883; *Dicranurus* Conrad 1841; *Miraspis* Richter & Richter, 1917; *Selenopeltoides* Prantl & Přibyl, 1949.

STRATIGRAPHICAL RANGE. Lower Ordovician (Arenig) to the Lower Devonian.

REMARKS. This group is equivalent to the *Selenopeltis* group of Ramsköld (1991b; here, *Selenopeltis* was used as the outgroup and so is excluded). The subfamilial name Selenopeltinae Hawle & Corda, 1847 cannot be used here as *Selenopeltis* falls outside the grouping: the subfamily Miraspinae Pollitt, 2006 is erected.

Subfamily **APIANURINAE** Whittington, 1956a

EMENDED DIAGNOSIS. L3 absent (ch. 4*; homoplastic character state). Eyes are positioned opposite posterior part of L1 (ch. 24; homoplastic character state). Prominent, elongate border spines present (ch. 27*; homoplastic and not known in *Boedaspis*). Hypostome widest anteriorly (ch. 33; seen also in *Exallaspis* and *Taemaspis*). Middle furrow of hypostome is triangular depression (ch. 34). Ten thoracic segments (ch. 37*; unknown in *Calipernurus* and *Apianurus*). Little/no differentation of thoracic segments (ch. 38*; unknown in *Calipernurus* and *Apianurus*). No posterolateral furrows defining posterior band in thorax (ch. 40*; homoplastic character state). Anterior pleural spine of thoracic segment is hook-like, posterior pleural spine long (ch. 47*; Not known in *Apianurus*. *Boedaspis* displays the homoplastic character state of having both pleural spines laterally-directed like *Odontopleura*). Antero-lateral part of axial thoracic ring is not inflated (ch. 43; many derived taxa display this state). Three pairs of internal border spines on pygidium (ch. 52; *Calipernurus* has 2 pairs). Width less than 2.2 times the length of the pygidium (ch. 53*; the pygidium of *Calipernurus* is over 2.5 wider than long).

TAXA INCLUDED. *Apianurus* Whittington, 1956a; *Boedaspis W*hittington & Bohlin, 1958; *Calipernurus* Whittington, 1956a.

STRATIGRAPHICAL RANGE. Lower Ordovician (Arenig) to Upper Ordovician (Ashgill).

REMARKS. The subfamilial status of this grouping (see Whittington 1956a and Whittington & Bohlin 1958) is confirmed here.

Genus **HISPANIASPIS** Hammann, 1992

[*Subfamilia incertae sedis*]

EMENDED DIAGNOSIS. No median occipital tubercle (ch. 8). Librigenae border spines tiny (ch. 27; seen in the more derived acidaspines also). Posterior border of pygidium is present abaxially to pleural ridge (ch. 49).

TYPE SPECIES. *Hispaniaspis morenaica* Hammann, 1976.

STRATIGRAPHICAL RANGE. Upper Ordovician.

Genus **ISOPRUSIA** Bruton, 1966a

[*Subfamilia incertae sedis*]

EMENDED DIAGNOSIS. Median occipital spine (ch. 8). Deep longitudinal glabella furrows (ch. 14). Three convex, forward lobes on anterior margin of cranidium (ch. 20).14-15 border spines on librigenae (ch. 29). Anterior pleural spine laterally directed with small spines, posterior pleural spine long and backwardly directed with no associated spines (ch. 42). Pygidial median border spine shorter than axis (ch. 50). 11 pairs of exterior pygidial spines (ch. 51).

TYPE SPECIES. *Isoprusia mydlakia* Bruton 1966a.

STRATIGRAPHICAL RANGE. Middle Devonian.

Genus **RINCONASPIS** Baldis & González, 1981

[*Subfamilia incertae sedis*]

EMENDED DIAGNOSIS. Strongly defined occipital lobes (ch. 16). Sharp and deep occipital furrow (ch. 17). Librigenal spine directed horizontally, backward and outward (ch. 30).

TYPE SPECIES. *Rinconaspis santiaguensis* Baldis & González, 1981.

STRATIGRAPHICAL RANGE. Lower Devonian.

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5. The phylogeny of the Illaenoidea (Trilobita)

5.1 INTRODUCTION AND TAXOMONIC HISTORY

THE phylogeny of this trilobite group has concerned many trilobite workers over the last fifty years or so. There is a large range of opinions about the systematic position of the group and its constituent groups. A comprehensive and valuable discussion highlighting the systematic problems surrounding this group was presented by Lane and Thomas (1983). More recent questions were raised by Whittington (2000). This chapter aims to examine differing opinions and to include a broad selection of scutelluid taxa into a phylogenetic analysis to see if a consensus can be obtained: this group is 'in need of comprehensive phylogenetic analysis' (Adrain *et al.* 1995).

Many early workers classified this group into only two genera with many sub-genera (e.g. Barrande 1852, 1872; Billings 1859; Hall 1847, 1868; Holm 1882, 1886; Reed 1904, 1906, 1914, 1935). Later workers tended to split these taxa into varying number of genera (for a history of classification, see Lane and Thomas (1983; p. 143)).

The two main groups, the styginids and the illaenids, have been divided by the presences of glabellar furrows, radiating ribs in the pygidium and broad pygidial doublure in the former group. The latter group has commonly been divided into two groups: those that display a rostal prominence and those that do not.

Effacement is common within the illaenids and often as a complex character-state (Lane & Thomas 1983). The morphological manifestations are: reduced distinctness of axial and/or pleural furrows of the dorsal surface; increased exoskeletal convexity; and increase in the relative width of the axis. It is with these effaced genera that there is most taxonomic controversy.

Prantl and Přibyl (1947) were the first workers to consider the styginid taxonomic issues critically. They regarded the phylogeny of the group as a continuous evolutionary

branch from the species *Scutellum (Scutellum) costatum*: separating into various *Scutellum (Scutellum)* groups throughout the Silurian and *Paralejurus* at the Silurian/Devonian boundary and then finally differentiating into *Kolihapeltis* and *Thysanopeltis* (from *Spiniscutellum*).

Šnajdr (1960) considered *Planiscutellum* to have given rise to *Kosovopeltis* and *Decoroscutellum* - *Spiniscutellum*. *Platyscutellum* and *Poroscutellum* both arose from *Spiniscutellum* as blind evolutionary branches.

Prantl and Přibyl (1947) considered *Thysanopeltis* to have arisen from *Spiniscutellum* whereas Richter and Richter (1956) thought *Thysanopeltis* was derived directly from *Scabriscutellum* (although all these taxa are considered closely-related; Richter & Richter 1956).

Due to an inability to 'recognize phyletic lines of development', Lane and Thomas (1983) did not identify subfamily divisions. Groupings have been alluded to (Ludvigsen & Tripp 1990; Adrain *et al.* 1995; Nielsen 1995): but few characters have been indicated to justify these groupings. This study hopes to provide some robust reasoning to any groupings and give future workers some indication of those character states that prove constructive.

5.2 PHYLOGENETIC ANALYSIS

5.2.1 TAXOMIC SAMPLING

Any highly-effaced group, such as this one, will supply considerably fewer obvious dorsal character states and, hence, will be harder to analyse with phylogenetic programs than other highly character-rich groups. Moreover, the ventral surfaces are not always exposed. Many taxa had to be excluded from the analysis in order to render it a feasible exercise. Any putative subspecies were coded as if they held species rank: the subspecies may not fall together closely when placed into context with all other taxa. Sixty-nine taxa were included in the final analysis (see Table 5.1 below; see Plate 6 for some sample taxa).

Genus	Coded species	Genus author and publication date
Alceste	*latissima*	Hawle & Corda 1847 (Shaw 2000; Bruthansová 2003)
Ancyropyge	*Acidaspis romingeri* Hall & Clarke, 1888	Clarke 1892 ((Ormiston 1967; Whittington 2000)
Avascutellum (=Ctenoscutellum; =Rutoscutellum)	*Bronteus edwardsi* Barrande, 1852	Šnajdr 1989
Bojoscutellum (=Holomeris; =Breviscutellum)	*Bronteus paliferum* (Beyrich, 1845)	Šnajdr 1958
Bronteopsis (=Homoglossa)	*scotica*	Etheridge & Nicholson *in* Nicholson & Etheridge 1879
Bumastoides	*Illaenus milleri* Billings, 1859	Whittington 1954 (Lane & Thomas 1983)
Bumastus (Bumastella)	*Bumastus (Bumastella) spiculus*	Kobayashi & Hamada 1974
Bumastus (Bumastus)	*barriensis*	Murchison 1839
Calycoscutellum	*Bronteus flabellifer* Goldfuss, 1839	Archinal 1994
Cavetia	*hoplites*	Feist 1974
Cekovia	*Illaenus transfuga* Barrande, 1852	Šnajdr 1956 (Bruthansová 2003)
Cornuscutellum	*Bronteus rhinoceros* Barrande, 1872	Šnajdr 1960 (Holloway 1996)
Cybantyx	*anaglyptos*	Lane & Thomas *in* Thomas 1978 (Lane & Thomas 1983; Whittington 1997)
Decoroscutellum (Decoroscutellum)	*Bronteus haidingeri* Barrande, 1846a	Šnajdr 1960 (Ormiston 1968)
Dentaloscutellum	*hudsoni*	Chatterton 1971
Dulanaspis	*levis*	Chugaeva 1956
Dysplanus	*Asaphus (Illaenus) centrotus* Dalman, 1827	Burmeister 1843
Ectillaenus (=Wossekia)	*Illaenus? Perovalis* Murchison, 1839	Salter 1867 (Bruthansová 2003)
Eobronteus	*Entomostracites laticauda* Wahlenberg, 1821	Reed 1928 (Whittington 1950, 2000)

Eokosovopeltis	*Bronteus romanovskii* Weber, 1948	Jaanusson 1953 (Edgecombe *et al.* 2004)
Exastipyx	*Weberopeltis maksimovae* Feist, 1974	Holloway 1996
Excetra	*iotops*	Holloway & Lane 1998
Failleana (=Opsypharus)	*calva*	Chatterton & Ludvigsen 1976 (Lane & Thomas 1983, Whittington 1997)
Harpillaenus	*Illaenus arcuatus* Billings, 1865	Whittington 1963
Illaenus (/Cryptonymus; =Actinolobus; =Deucalion; =Svobodapeltis)	*sarsi*	Dalman 1827 (Hu 1971; Whittington 1997)
Izarnia	*Bronteus gouzesi* Bergeron, 1889	Feist 1974 (Vanêk *et al.* 1992)
Kolihapeltis	*Bronteus parabolinus* Barrande, 1882	Prantl & Přibyl 1947
Kosovopeltis (=Eokosovopeltis; =Heptabronteus) (Scutelluinae)	*svobodai*	Šnajdr 1958 (Webby 1974; Ludvigsen & Tripp 1990; Kăcha & Šarič 1991)
Lamproscutellum	*guizhouense*	Yin 1980 (Edgecombe *et al.* 1994)
Ligiscus	*arcanus*	Lane & Owens 1982
Liolalax (/Lalax)	*Lalax olibros* Holloway & Lane, 1998	Holloway & Lane 1999
Litotix	*Illaenus armatus* Hall, 1865	Lane & Thomas *in* Thomas 1978
Meridioscutellum	*Bronteus meridionalis* Barrois, 1886	Feist 1970 (Holloway 1996)
Meroperix	*ataphrus*	Lane 1972
Metascutellum	*Bronteus pustulatus* Barrande, 1846a	Šnajdr 1960
Nanillaenus	*mackensiensis*	Chatterton 1980 (Whittington 1997)
Octillaenus	*Illaenus hisingeri* Barrande, 1846b	Salter 1867 (Bruton & Owens 1988; Bruthansová 2003)
Opoa	*adamsi*	Lane 1972
Ottenbyaspis	*Illaenus oriens* Moberg & Segerberg, 1906	Bruton 1968

Panderia (/Rhodope)	*parvula*	Volborth 1863 (Bruton 1968)
Paracybantyx	*occidentalis* Adrain *et al.*, 1995	Ludvigsen & Tripp 1990 (Adrain *et al.* 1995)
Paralejurus	*tenuistriatus* Schraut & Feist, 2004	Hawle & Corda 1847 (Schraut & Feist 2004)
Parillaenus	*Illaenus fallax* Holm, 1882	Jaanusson 1953 (Bruton & Owens 1988)
Perischoclonus	*capitalis*	Raymond 1925
Phillipsinella	*Phacops parabola* Barrande, 1846b	Novák 1885 (Bruton 1976)
Planiscutellum (=Protoscutellum)	*Bronteus (Holomeris) planus* Hawle & Corda, 1847	Richter & Richter 1956
Platillaenus	*Illaenus ladogensis* Holm *in* Schmidt, 1886b	Jaanusson 1953
Platyscutellum	*Bronteus formosus* Barrande, 1846a	Šnajdr 1958
Poroscutellum	*Bronteus porosus* Barrande, 1846a	Šnajdr 1958
Raymondaspis (/Warburgella Raymond)	*reticulatus*	Whittington 1965 (Skjeseth 1955; Fortey 1980)
Rhaxeros (=Rhax)	*Rhax pollinctrix* Lane & Thomas, 1978	Lane & Thomas 1980 (Holloway & Lane 1998)
Scabriscutellum (=Dicranactis)	*Bronteus scaber* Goldfuss, 1843	Richter & Richter 1956 (Archinal 1994)
Scutellum (=Bronteus/Brontes; =Goldfussia/Brontes; =Goldius)	*costatum*	Pusch 1833 (Archinal 1994)
Snajdria	*foveolata*	Hammann 1992
Spiniscutellum	*Bronteus umbellifer* Beyrich, 1845	Šnajdr 1960
Stenopareia	*glaber*	Owen & Bruton 1980 (Whitttington 1997; Ludvigsen & Tripp 1990; Bruthansová 2003)
Stygina	*Asaphus latifrons* Portlock, 1843	Salter 1853 (Whittington 2000)
Thaleops	*ovata*	Conrad 1843 (Sinclair 1947)
Theamataspis	*illaenoides*	Öpik 1937
Thomastus	*thomastus*	Öpik 1953
Thysanopeltis	*speciosa*	Hawle & Corda 1847 (Prantl & Přibyl 1947)

Turgicephalus	*falcatus*	Fortey 1980
Ulugtella	*turgida*	Petrunina in Repina *et al.* 1975 (Hammann 1992; Bruthansová 2003)
Waisfieldaspis	*beatrizae*	Vaccari 2001
Weberopeltis	*Bronteus (Thysanopeltis) aculeatus* Weber, 1945	Maksimova *in* Moore 1959 (Ellermann 1992; Ormiston 1967)
Xyoeax	*eponcus*	Holloway 1996
Zbirovia	*Illaenus aratus* Barrande, 1872	Šnajdr1956 (Hammann 1992; Bruthansová 2003)
Zdicella	*Illaenus zeidleri* Barrande, 1872	Šnajdr1957 (Bruthansová 2003)
Zetillaenus	*Illaenus wahlenbergianus* Barrande, 1952	Šnajdr1957 (Bruthansová 2003)

Table 5.1: A list of all taxa included in the analysis. References are given for type species; other important literature is referenced in brackets.

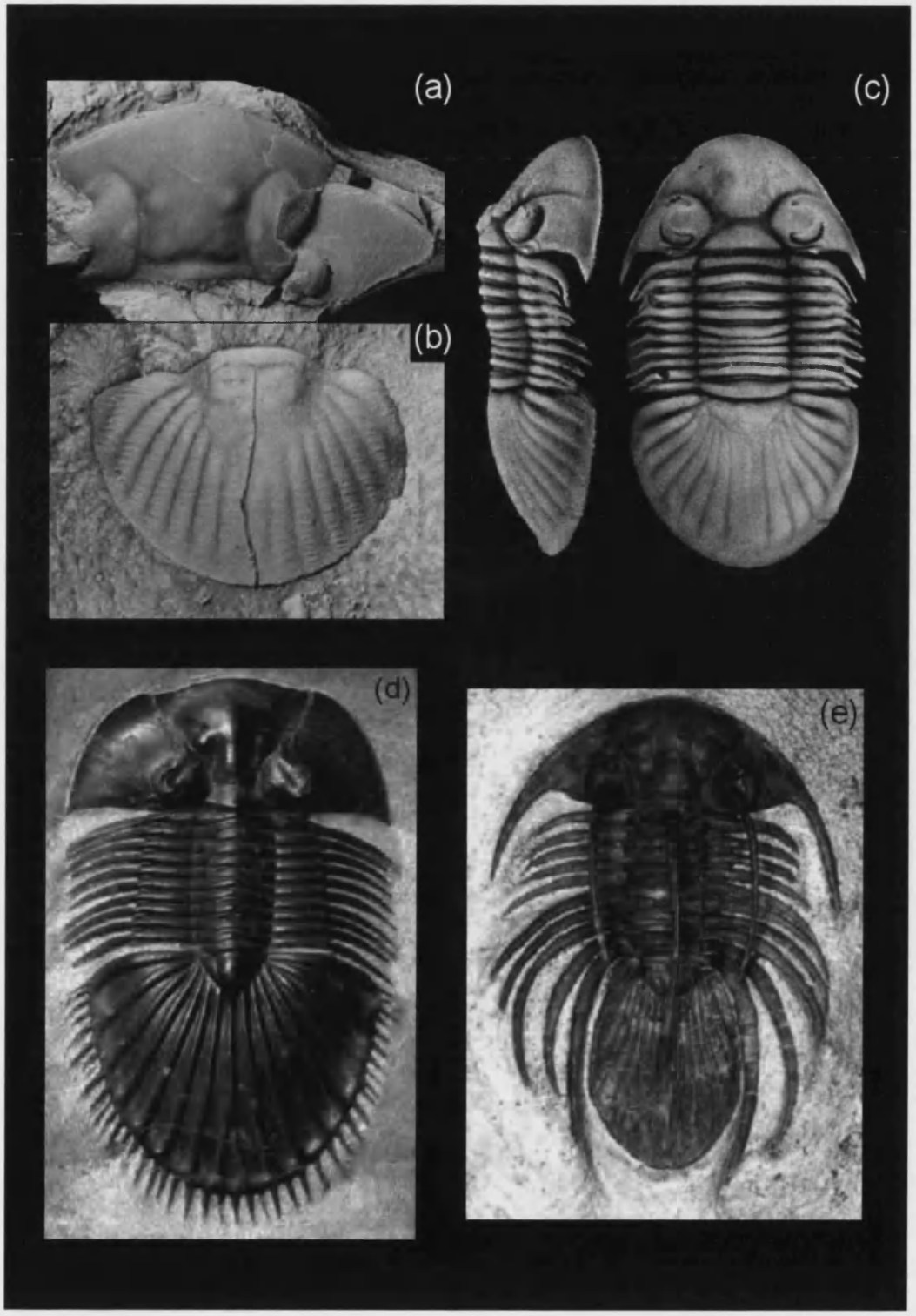

Plate 6

Plate 6.
(a) Cranidium and (b) pygidium of *Eokosovopeltis grandicurvatus* Edgecombe *et al.*, 1994; Fig 4 (A) and 5 (D) respectively; x 2.5; (c) *Paralejurus tenuistriatus* Schraut & Feist, 2004; Figure 7 (pts 6 and 7); x 2.0; (d) *Thysanopeltis* sp. (www.trilobites.info); x 2.0; (e) *Kolihapeltis* sp. (www.trilobites.info); x 2.0).

5.2.2 METHODS

The dataset from Appendix III was analyzed using PAUP (version 4.0b10*, Swofford 2002). See section 3.3.2 for full description of methods (i.e. PTP, bootstrap, ACCTRAN, TreeRot, MacClade and section 4.2.2 for Parsimony Ratchet). All ninety-nine characters were equally weighted. Characters 15, 56 and 78 were treated as ordered: all others were unordered (see *Characters* section below). The dataset includes no phylogenetically-uninformative characters.

5.2.2.1 *Outgroup*

Raymondaspis was used as the outgroup. This genus is stratigraphically-old and characterises several evolutionarily-primitive features: (1) the simple, flat exoskeleton and simply-formed doublure; (2) the moderately concave, wide preglabellar depression; (3) three pairs of single lateral glabellar impressions; (4) pygidial ribs are moderately vaulted; (5) very narrow inter-pleural furrows and (6) a long pygidial axis that persists along nearly the full length of the pygidium (see Šnajdr 1960).

5.2.2.2 Character coding

Well-preserved rostral plates and hypostomata are known for relatively few taxa. However, rostral plates and hypostomata have long been considered important for illaenid classification (Jaanusson 1953; Šnajdr 1960) and, in light of this, it was deemed important to include them in the analysis.

Extreme care has been taken to be consistent and determine the character state from *either* the dorsal *or* the ventral side of the exoskeleton, according to the character being coded (specified in the character list). Not all authors have made this distinction (e.g. Prantl & Přibyl (1947) has not; *cf.* Šnajdr 1960). The terminology of Whittington (1999) is used: please refer to his figure 1 for diagrammatical clarification.

Taxon	Paper(s) that describe ontogenetic stages
Alceste	Hammann 1992
Bumastella	Holloway & Lane 1998
Bumastoides	Chatterton 1980
Cekovia	Hammann 1992
Dentaloscutellum	Chatterton 1971
Failleana	Chatterton & Ludvigsen 1976
Illaenus	Hu 1971
Kosovopeltis	Ludvigsen & Tripp 1990
Nanillaenus	Chatterton 1980
Parillaenus	Hammann 1992
Perischoclonus	Whittington 1963; Lane & Thomas 1983
Scutellum	Chatterton 1971

Table 5.2: Known illaenoid ontogenies.

5.2.2.3 Ontogeny

Several ontogenies are known – most from the later meraspid stages rather than the earliest stages (see Table 5.2). Ten ontogenetic stages of *Zdicella* were described at a lecture by Novak in 1876 but are considered currently lost (see Bruthansová 2003, p. 186).

5.2.2.4 Character list

Whole exoskeleton

1. Ornamentation:
    0. Scattered pits between terrace ridges, may be of two sizes, e.g. illaenids
    1. Fine pitting/punctae over cranidium surface, e.g. *Illaenus*, *Zbirovia*
    2. Prominent terrace ridges, e.g. *Eobronteus*
    3. No discernible surface sculpture, e.g. *Bumastus*
    4. Distinctive surface tubercles, e.g. *Metascutellum*

Cranidium

2. 1S glabellar furrows:
    0. Absent (Early illaenid *Illaenus sarsi*)
    1. Present (scutelluids)
    2. Present as muscle scars e.g. *Raymondaspsis*, *Bronteopsis*, *Theamataspis*
3. 2S glabellar furrows:
    0. Absent (Early illaenid *Illaenus sarsi*)
    1. Present (scutelluids)
    2. Present as muscle scars e.g. *Raymondaspsis*, *Bronteopsis*, *Theamataspis*

4. S2 glabellar furrow:
    0. Subcircular
    1. Transverse

5. 3S glabellar furrows:
    0. Absent (Early illaenid *Illaenus sarsi*)
    1. Present as a furrow (scutelluids)
    2. Present as muscle scars e.g. *Raymondaspsis*, *Bronteopsis*, *Theamataspis*
    3. Pit-like, e.g. early scutelluid *Perischoclonus*

6. Connection of the glabellar furrow 1S to the axial furrow:
    0. Present (styginids and scutelluids)
    1. Absent; isolation of the glabellar muscle areas from the axial furrow (illaenids)

7. Connection of the glabellar furrow 2S to the axial furrow:
    0. Present (styginids and scutelluids)
    1. Absent; isolation of the glabellar muscle areas from the axial furrow (illaenids)

8. Connection of the glabellar furrow 3S to the axial furrow:
    0. Present, faint shallow connection (styginids and scutelluids)
    1. Absent; isolation of the glabellar muscle areas from the axial furrow (illaenids)

9. Anteromedial node in S1 (Holloway 1996):
    0. Absent
    1. Present, e.g. *Ancyropyge* and *Weberopeltis*

10. S1 glabellar furrows:
    0. Bifurcate, e.g. early scutelluid *Perischoclonus*
    1. Not bifurcate

11. Small, deep anteromedial pit in L1, as an additional muscle attachment point (Šnajdr 1960, fig. 4; Whittington 1999, fig. 2.7):
    0. Absent
    1. Present, e.g. *Decoroscutellum* and *Theamataspis* (Fortey 1980)

12. S1 bifurcate: centre occupied by a small median node (Whittington 1999):
    0. Present and strong, e.g. the Devonian *Scutellum*
    1. Present but faint, e.g. the stratigraphically old Ordovician *Eobronteus* and Silurian *Planiscutellum*

13. Median node, if present, is:
    0. Small, low and smooth, e.g. *Scabriscutellum*
    1. Larger and bears the external sculpture of the rest of the glabella, e.g. *Bojoscutellum*

14. L2-L3:
    0. Not inflated
    1. Inflated, e.g. *Bojoscutellum*

15. Longitudinal glabellar furrow (inner ends of S1 and S2 connected by an exsagittally-directed furrow; see Whittington 1999, p. 415):

0. Absent
1. Present (e.g. *Scabriscutellum*, faint in *Bojoscutellum*)
2. Extends forwards to the adaxial end of S3 (i.e. the stratigraphically young *Thysanopeltis*)

16. Occipital furrow:
    0. Present (Styginidae)
    1. Absent or very weak (Early illaenid *Illaenus sarsi* and other illaenids)

17. Medial enlargement of the occipital ring:
    0. Absent, e.g. *Spiniscutellum*
    1. Present, may be slight, e.g. *Decoroscutellum* and *Bojoscutellum,* slight in *Kosovopeltis*

18. Lateral occipital lobe (Whittington 1999, p. 414):
    0. Absent
    1. Present (e.g. *Poroscutellum*, faint in *Spiniscutellum* and *Kosovopeltis*)

19. Posterior border furrow on librigena:
    0. Absent (illaenids)
    1. Present

20. Lateral border furrow on librigena:
    0. Absent
    1. Present

21. Strong inflation of the inner, posterior corner of the fixigena: posterior border furrow lies close to the margin proximally (see Whittington 1999):
    0. Absent
    1. Present, e.g. *Avascutellum*, *Spiniscutellum* and *Decoroscutellum*

22. Vincular fold in posterior edge of cheek doublure (see Whittington 1997, fig. 5.6):
    0. Present (illaenids; *Dentaloscutellum* and *Scutellum* (see Whittington 1999)

1. Absent

23. Eye lobe:
    0. Far back on cheek and close to axis (Styginidae)
    1. Far out on cheek, near posterior border, e.g. *Bumastus*, *Illaenus*

24. Eye size:
    0. Large (>40% of whole length of cranidium)
    1. Medium (25-40%)
    2. Small (<25%)
    3. Absent, e.g. *Thomastus*

25. Palpebral lobes (e.g. Kaelser 1997, fig. 5.2):
    0. Present, e.g. *Calycoscutellum*
    1. Absent, e.g. *Thomastus*

26. Orientation of palpebral lobes (width of palpebral lobes difficult to measure and code discretely, but this character allows the coding of nature of the eyes without attempting to quantify width (Amati & Westrop 2004)):
    0. Horizontal or slightly ventrally directed
    1. Directed upward ('stalk-like', as in *Thaleops ovata*)

27. Palpebral spines:
    0. Absent
    1. Present as low nodes, e.g. *Kosovopeltis* (Whittington 1999)
    2. Present, e.g. *Bojoscutellum* and *Decoroscutellum* (Whittington 1999)

28. Eye ridges:
    0. Present, e.g. *Bojoscutellum*
    1. Absent, e.g. *Alceste*

29. Glabella:
    0. Entirely well-defined (Scutelluina)
    1. Defined past eye-lobes, but weakly anteriorly, e.g. *Scabriscutellum*

2. Not defined anteriorly to eye-lobes, e.g. *Hapillaenus*
3. Outlined by shallow, dorsal furrows that diverge outwards and forwards from posterior margin (i.e. *Panderia*; see Bruton 1968)

30. Glabella:
    0. Anterior expansion slight; two parallel/slightly diverging rows of scars, e.g. *Perischoclonus, Illaenus*, *Bumastoides*, *Stenopareia*, *Thaleops* + Ectillaeninae
    1. Anterior expansion great - waisted glabella; more anterior pairs are increasingly farther from sagittal line – therefore greater anterior expansion, e.g. *Bronteopsis*, *Raymondaspis, Bumastus*, *Dysplanus* and *Failleana*

31. Median glabellar node, present on glabella at the level of L2/palpebral lobes:
    0. Present, e.g. *Ottenbyaspis*, *Poroscutellum* and *Bojoscutellum*
    1. Weak, e.g. *Illaenus consimilis*
    2. Absent, e.g. *Scutellum*

32. Anterior pit/boss (the *omphalus* of Holloway & Lane 1998; dorsal reflection of a ventral process positioned at the anterolateral corner of the glabella close to where the 3S glabellar furrow meets the axial furrow. This character is very dependent on preservation condition but it was important to code it where known):
    0. Present, e.g. *Stygina*, *Raymondaspis, Bumastus*, *Dysplanus* and *Failleana*
    1. Absent, e.g. illaenids (*Nanillaenus*, *Bumastoides*, *Panderia*), *Illaenus*, *Bumastoides*, *Stenopareia*, *Thaleops* and Ectillaeninae

33. Anterior node (the 'anterolateral internal pit' of Holloway & Lane 1998; a small pit in the internal surface of the exoskeleton that is situated between the anterior pit/*omphalus* and cephalic margin. On internal molds this is a small node and on external molds this is a barely raised spot that interrupts the sculpture of the terrace ridges (Whittington 1997, p. 880)):
    0. Present, e.g. *Cybantyx*

1. Absent

34. Fixigenal impressions (lunettes) (Whittington 1999):
    0. Present, e.g. Illaenids, styginids and *Phillipsinella*
    1. Absent, e.g. *Panderia* sp.

35. Librigenal spines (after Amati & Westrop 2004):
    0. Present, directed posteolaterally with subgenal notch, e.g. *Thaleops ovata*
    1. Present, directed backwards without sub-genal notch, e.g. *Raymondaspsis vespertina* Fortey, 1980; pl.6, fig. 6
    2. Reduced to an elongated flap-like form, e.g. *Paracybantyx*
    3. Reduced to a rounded genal angle, e.g. *Illaenus*

36. Anterior sutures (from γ to α; general trend from anterior of eye lobes toward the anterior border - not where the suture bisects the anterior border itself):
    0. Subparallel
    1. Distinctly divergent, e.g. Illaenina
    2. Distinctly convergent

37. Anterior border and furrow:
    0. Present
    1. Absent

38. Preglabellar area:
    0. Present: flat, forward and slowly downwards sloping, e.g. *Bronteus*; may be tiny as in *Bronteopsis* and *Kolihapeltis*
    1. Absent: spherical and suddenly downwards sloping, e.g. *Scutellum*

39. Occipital tubercle:
    0. Absent, e.g. *Alceste*
    1. Present, e.g. *Bronteopsis*
    2. Present as a stout or short spine, e.g. *Bojoscutellum* and *Decoroscutellum*

3. Present as a long spine, e.g. *Cornuscutellum*

40. Occipital tubercle bearing four pits arranged at the corners of a square (occipital organ):
    0. Absent
    1. Present, e.g. *Paralejurus*, *Bronteopsis* and *Raymondaspis*

41. Median glabellar node/spine opposite S3:
    0. Absent
    1. Present, e.g. *Izarnia*
    2. Present as a spine, e.g. *Weberopeltis* (Feist 1974)

Hypostome and rostral plate

42. Rostral flange (a notched anterior margin of hypostome implies a median projection of the cranidial doublure, as the hypostome fitted against the inner margin of the cephalic doublure. This projection was probably formed by axe-shaped rostral flange (Whittington 1965, p. 385): therefore the outline of the anterior margin of the hypostome can be used to argue for the presence of the rostral flange when the rostral plate is unknown. It is important to note that care must be exercised when using the presence/absence character state of the rostal flange to define higher (subfamilial and familial) taxa: its presence is almost certainly a convergent character state (Lane & Thomas 1983, p. 149):
    0. Present (*Panderia*, *Bumastus*, *Stenopareia* and *Illaenus*)
    1. Absent

43. Posterior points of the rostral plate:
    0. Dorsally bent, e.g. *Scutellum* and *Paralejurus*
    1. Not dorsally bent

44. Hypostome middle body:
    0. Oval, e.g. *Illaenus*
    1. Long and narrow, i.e. *Phillipsinella*
    2. Extremely short posterior lobe, e.g. *Scutellum*

3. Transversely elongate, e.g. *Stenopareia*, *Zdicella*

45. Anterior wings:
    0. Large and quadrangular (illaenids)
    1. Narrow, e.g. *Stenopareia*

46. Maculae:
    0. Prominent (Styginidae; *Scutellum*-like)
    1. Small, insignificant

47. Connective sutures:
    0. Diverge at a high angle, e.g. *Dysplanus* and *Platillaenus*
    1. Diverge at low angle

Thorax

48. Number of thoracic segments (this has been thought to be a poor character (Lane & Thomas 1983, p. 150) but it was judged important to include it nevertheless):
    0. 6, e.g. *Phillipsinella*
    1. 7
    2. 8, e.g. *Octillaenus*, *Panderia*
    3. 9
    4. 10
    5. 11

49. Axial ring on thorax:
    0. Short (Late Ordovician styginids)
    1. Long *(Cybantyx anaglyptos)*

50. Articulating furrow:
    0. Present (scutelluids and Late Ordovician styginids)
    1. Absent *(C. anaglyptos)*

51. Doublure of axial ring:

0. Lies close to ring
1. Long and curves downward *(C. anaglyptos)*

52. Thoracic segments have a:
    0. Raised axial ring, shorter in the midline than laterally (scutelluids)
    1. Not like above (illaenids)

53. Half-ring:
    0. Extending horizontally forward beneath the ring in front (scutelluids)
    1. No discrete half-ring present, e.g. *Rhaxeros*, *Bumastus* and *Cybantyx*

54. Pleurae are:
    0. Fulcrate process and socket (scutelluids)
    1. Non-fulcrate (illaenids)

55. Thoracic pleurae:
    0. Outer portion with facet and doublure extending in close to fulcrum (Kosovopeltinae)
    1. Large fulcral process on first segment, smaller on successive segments, e.g. *Planiscutellum*

56. Pleural furrow:
    0. Absent (Late Ordovician styginids, *Illaenus*, *Nanillaenus*, *Thaleops*, *Ectillaenus* and early illaenid *Illaenus sarsi*)
    1. Present as a slight slope or on internal moulds only, e.g. *Bronteopsis*
    2. Present as a distinct furrow, e.g. *Thysanopeltis*

57. Axial furrows of thorax:
    0. Posteriorly divergent, e.g. *Paralejurus*
    1. Roughly parallel, e.g. *Thysanopeltis*
    2. Convergent, e.g. *Thomastus*
    3. Not visible, e.g. *Bumastus*

58. Depth of axial furrows:
    0. Shallow, e.g. *Cybantyx*
    1. Deep, e.g. *Bronteopsis*

59. Axis (or convexity representing axis) as a function of thoracic width:
    0. <1/3, e.g. Silurian/Devonian scutelluids, *Stygina* and *Spiniscutellum*
    1. ≥1/3, e.g. illaenid genera, e.g. *Illaenus*, *Nanillaenus*, *Thaleops*, *Ectillaenus*

60. Pleural tips:
    0. Spinose, e.g. *Thysanopeltis*
    1. Rounded and blunt, e.g. *Bumastus*
    2. Gently curved posteriorly, e.g. *Planiscutellum*

Pygidium

61. Maximum length (sag.) of pygidium (excluding spines) relative to maximum width (tr.) (the length/width ratio of the pygidium may be a poor character to use in a generic-level analysis as ratio changes substantially (increases) in the ontogeny of *Failleana calva* (Chatterton & Ludvigsen 2004) – but the character states used here are loose and may, nevertheless, provide important information):
    0. Pygidium wider (tr.) than long (sag.), e.g. *Bronteopsis*
    1. As long as wide, or longer than wide, e.g. scutelluines, *Parillaenus fallax*, *Kolihapeltis*

62. Size of pygidium compared to the cranidium:
    0. Smaller and less convex
    1. Equal
    2. Larger

63. Marginal spine expression of pygidium:
    0. Lacks marginal spines, e.g. Scutelluina
    1. Possesses marginal spines, not related to the pleural ribs, e.g. *Thysanopeltis*

2. Possesses marginal spines that are continuations of the pleural ribs, e.g. *Dentaloscutellum* (Šnajdr 1960, pl. 29, fig. 2; Chatterton 1971), *Weberopeltis*

64. Spine thickness:
    0. Uniform, e.g. *Dentaloscutellum*
    1. Non-uniform, e.g. *Ancyropyge* and *Xyoeax* (see Holloway 1996, p. 433)

65. Pygidial pleural field adaxial to border:
    0. Long, i.e. *Thysanopeltis*
    1. Narrow, i.e. *Weberopeltis* (see Holloway 1996, p. 433)

66. Radiating ribs on pygidium:
    0. Present (scutelluids)
    1. Absent (illaenids)

67. Pygidial ribs:
    0. Low and broad in profile
    1. Appear as narrow prominent ridges, e.g. *Thysanopeltis* and *Scabriscutellum*

68. Number of ribs:
    0. <5 pairs, e.g. *Phillipsinella*
    1. 6 pairs, e.g. *Eobronteus*
    2. 7 pairs, e.g. *Dentaloscutellum*
    3. 8 pairs, i.e. *Ligiscus* and *Perischoclonus*

69. Pygidial doublure:
    0. Very extensive (<3/4 length of whole pygidium) (scutelluids)
    1. Narrow (<1/3 total sagittal length) (illaenids)

70. Doublure:
    0. Anterior margin subparallel to the posterior margin of the pygidium (many Silurian and Devonian scutelluids)

1. Remote from this position, e.g. *Bumastus*, *Cybantyx* and *Failleana*

71. Anterior margin of doublure:
    0. Medially bears a forward projection, simple, e.g. *Illaenus*, *Bumastoides*, *Stenopareia*, *Thaleops* and Ectillaeninae (typically)
    1. Medially bears a forward projection, bifid, e.g. *Bumastoides*
    2. Does not bear a forward projection, e.g. *Bumastus*, *Dysplanus* and *Failleana* (styginids and scutelluids)

72. Doublure with ridges:
    0. Present, prominent, e.g. Scutelluina
    1. Absent

73. Posterior border furrow of pygidium:
    0. Present
    1. Absent (early illaenid *Illaenus sarsi*)

74. Lateral borders:
    0. Absent, e.g. Scutelluina
    1. Present, e.g. *Thomastus*

75. Pleural furrow of pygidium:
    0. Absent (early illaenid *Illaenus sarsi*, Illaeninae, and other illaenids)
    1. Present

76. Inter-pleural furrows on pygidium:
    0. Absent (illaenids)
    1. Present

77. Inter-ring (axial) furrows on pygidium:
    0. Present, e.g. *Perischolconus*
    1. Absent or faint (illaenids)

78. Degree of definition of pygidial axis:

0. Entirely well-defined, axial furrows are deeply incised and axis is highly vaulted, e.g. *Thaleops ovata*
1. Entirely weakly outlined by shallow furrows around the entire circumference of the axis, but not vaulted to a great degree above the pleural fields (as defined by Amati & Westrop 2004), e.g. *Nanillaenus*
2. Posterior portion of axial furrows effaced, posterior part of the axis obscurely marked off by a change in curvature, e.g. *Eobronteus*
3. Complete undifferentiated, possibly present on internal mold, e.g. *Bumastus*, *Stenopareia*

79. Axis:
    0. Relatively long, persisting along nearly the full length, e.g. *Phillipsinella*, *Raymondaspis*
    1. Relatively short, shorter than post-axial field, e.g. *Planiscutellum*, *Eobronteus*

80. Postaxial ridge:
    0. Developed, e.g. *Parillaenus*
    1. Short post-axial ridge on internal mould, e.g. *Phillipsinella*
    2. Absent, e.g. *Scutellum*

81. Medial flattened rib behind axis, separating pairs of ribs:
    0. Absent, e.g. *Scutellum*
    1. Present, e.g. *Poroscutellum*

82. Median rib:
    0. Not bifid or only marked with a obscure depression distally, e.g. an example of the latter expression is seen in *Eobronteus*
    1. Bifid: distally displaying a sagittal division by a furrow, e.g. *Dentaloscutellum*

83. Posteromedial pygidial rib extended into a pair of spines (each border spine is a prolongation of one of the two halves of the distal end of the median rib: only applicable to those taxa that are coded (82:1)):

0. Absent
1. Present, e.g. *Exastipyx* and *Dentaloscutellum* (Holloway 1996)

84. Axis as a function of anterior pygidial width:
0. <1/3, e.g. *Phillipsinella*
1. ≥1/3, e.g. illaenid genera, e.g. *Illaenus*, *Nanillaenus*, *Thaleops*, *Ectillaenus*

85. Anterior margin of pygidium:
0. Straight across
1. Straight medially, curves steeply downwards laterally, delimits the pygidium almost to a circle, e.g. *Rhaxeros*

86. *Holcos* (see Helbert *et al.* 1982):
0. Absent
1. Present, e.g. *Decoroscutellum*

87. Pygidial axis divided exsagittally into three portions:
0. Absent
1. Present (divided into 3 lobes - in stratigraphically young Scutelluinae – see Whittington 1999, e.g. *Bojoscutellum* and *Thysanopeltis*)

88. Node on pygidial axis (median portion of divided axis):
0. Absent
1. Present, e.g. *Izarnia*

89. Length and orientation of articulating facets (adopted from Amati & Westrop 2004):
0. Distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium 10–25% of total length (sag.) of pygidium
1. Distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium 25–50% of total length (sag.) of pygidium
2. Distance from anterior margin of pygidium to point of maximum width (tr.) of pygidium >51% of total length (sag.) of pygidium

Ontogeny

90. Pleural furrows of transitory pygidium:
    0. Absent
    1. Present, e.g. *Failleana* (Chatterton 1980, p. 28) and *Perischoclonus* (Lane & Thomas 1983, p. 150)

91. Median glabellar spine at meraspid stage:
    0. Present, e.g. *Kosovopeltis* (see Kăcha & Šarič 1991)
    1. Absent, e.g. *Scutellum*

92. Node on palpebral lobes:
    0. Present, e.g. *Kosovopeltis*
    1. Absent

93. Genal spine at meraspid stage:
    0. Present, e.g. *Bumastella* (Holloway & Lane 1998)
    1. Absent

94. Long occipital spine at meraspid stage that shortens throughout ontogeny:
    0. Present, e.g. *Dentaloscutellum* and *Kosovopeltis*
    1. Absent

95. Disappearance of the eye ridge throughout ontogeny:
    0. Present
    1. Absent, e.g. *Cekovia*

96. Border spines on transitory pygidium:
    0. Present, e.g. *Dentaloscutellum*
    1. Absent, e.g. *Cekovia*

97. Sub-transverse inter-ring furrows on axes of early pygidia:
    0. Present, e.g. *Dentaloscutellum*
    1. Absent, e.g. *Bumastella*

98. Axial spines of pygidia:
    0. Absent, e.g. *Nanillaenus*
    1. Only present on certain segments, e.g. *Dentaloscutellum*
    2. Present on all segments, e.g. *Scutellum*

99. Tuberculation pattern at early meraspid stage:
    0. Like *Dentaloscutellum*, *Scutellum* (see Chatterton 1971, fig. 4c and 6c)
    1. Like the illaenid trilobite protaspis (of Shaw 1968) and *Bumastoides* (see Chatterton 1980, fig. 4B and 4H respectively)
    2. No tubercles, as in *Failleana* and *Nanillaenus* (see Chatterton 1980, fig. 4D and 4I respectively)

5.2.3 RESULTS

The tree search found 39 most parsimonious trees with a length of 663 (CI 0.22, HI 0.79). They show the following relationships:

- Two large monophyletic clades with *Meroperix*, *Perischoclonus*, *Phillipsinella*, *Turgicephalus*, *Bronteopsis*, *Stygina* and *Raymondaspis* basally;
- One of the clades contains mostly styginids; and
- The other contains mostly illaenid taxa (see Figure 5.1).

Description and analysis of the phylogeny are based on the majority-rule tree (Figure 5.2). The main clades are classified here as followed:

- Clade A: Ectillaeninae;
- Clade B: Illaeninae;
- Clade C: Bumastellinae;
- Clade D: Panderiinae;
- Clade E: Kosovopeltinae; and
- Clade F: Thysanopeltinae (see section 5.5).

Character states with ambiguous optimisation are indicated by asterisks next to the character in question, within the *Systematic Palaeontology* section.

5.2.4 DISCUSSION

Characters that have phylogenetic importance (i.e. those with states that have a CI of 1.0) are:

- Presence/absence of anteromedial node in S1 (ch. 9);
- Presence/absence of lunettes (ch. 34);
- Presence/absence of occipital tubercle bearing four pits arranged at the corners of a square (ch. 40);
- Doublure of axial ring is close to ring or long and curves downward (ch. 51);
- Presence/absence of marginal spines of pygidium (ch. 63);
- Pygidial pleural field adaxial to border is long or narrow (ch. 65);
- Presence/absence of median glabellar node at meraspid stage (ch. 91);
- Presence/absence of genal spine at meraspid stage (ch. 93);
- Presence/absence of long occipital spine at meraspid stage that shortens throughout ontogeny (ch. 94);
- Disappearance of the eye ridge throughout ontogeny (ch. 95);
- Presence/absence of sub-transverse inter-ring furrows on axes of early pygidia (ch. 97);
- Presence/absence of axial spines of pygidia (ch. 98); and
- Tuberculation pattern at early meraspid stage (ch. 99).

The positions of *Paralejurus* and *Planiscutellum* may need further consideration. They have typical styginid pygidia albeit somewhat effaced: perhaps the taxa are grouped together by effacement and the resulting tree separates the effaced styginids and non-effaced styginids.

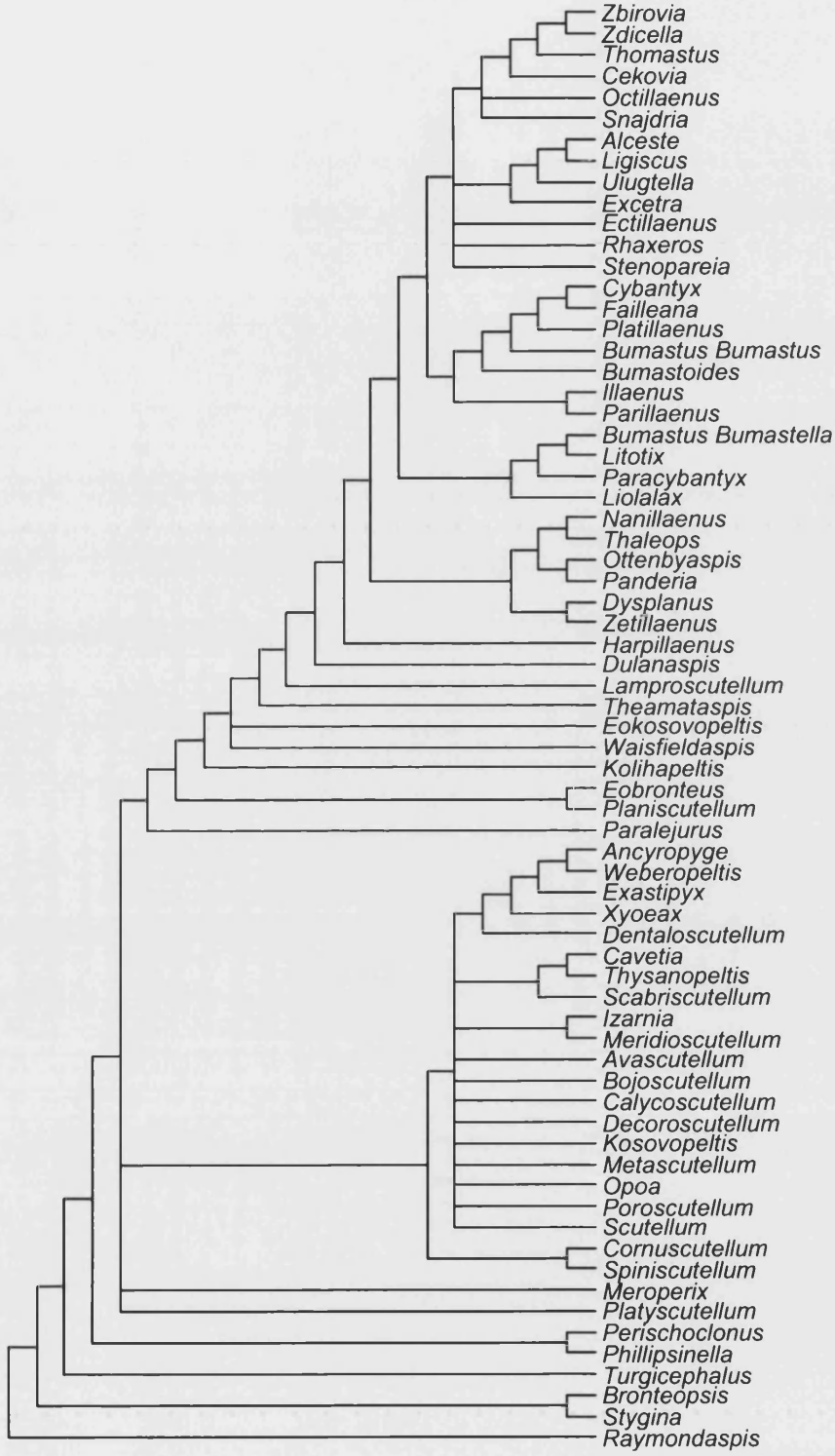

Figure 5.1: The strict-consensus tree.

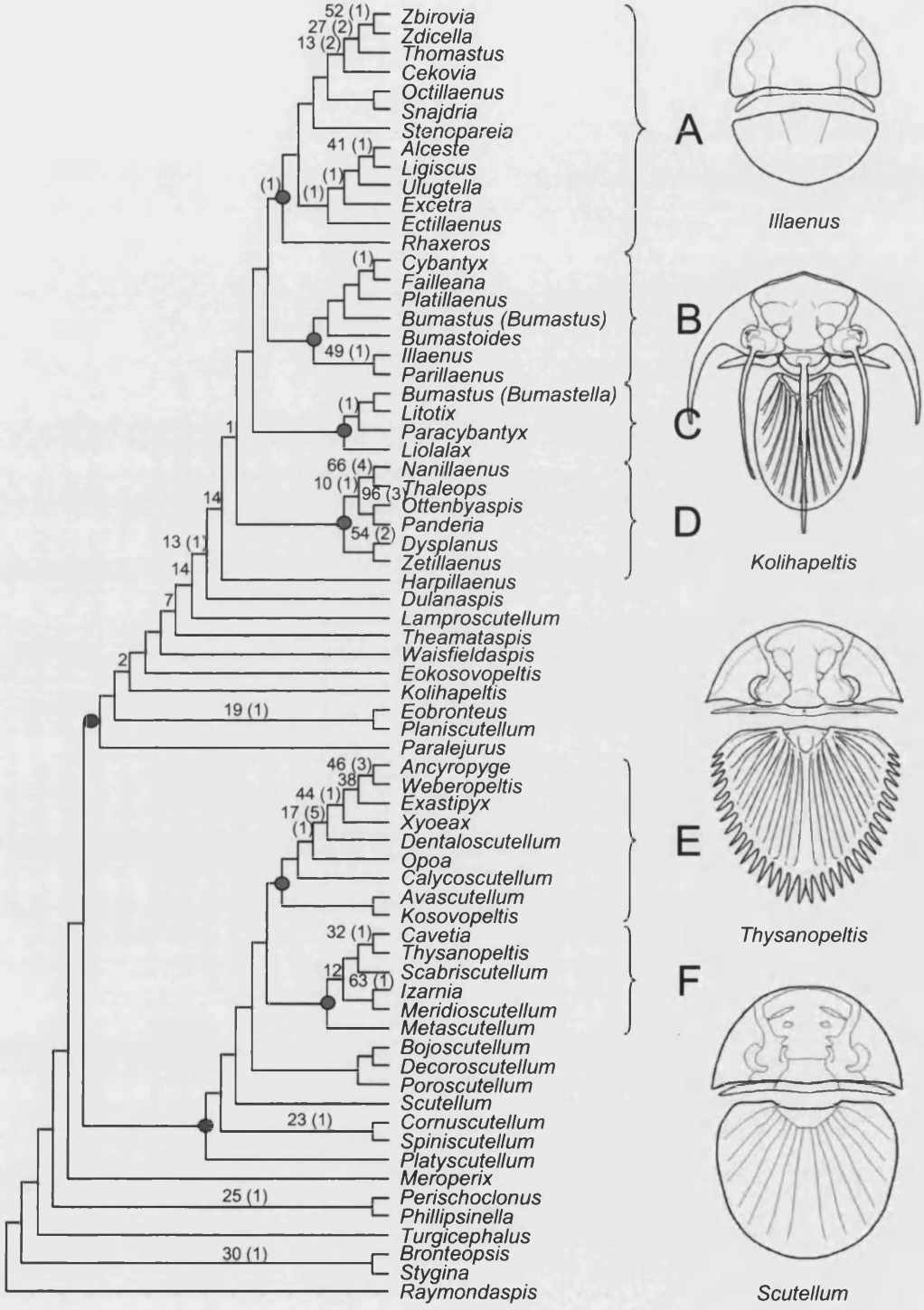
52 (1)
27 (2)
13 (2)
41 (1)
(1)
(1)
(1)
49 (1)
(1)
1
66 (4)
10 (1)
96 (3)
14
54 (2)
13 (1)
14
7
2
19 (1)
46 (3)
38
44 (1)
17 (5)
(1)
32 (1)
12
63 (1)
23 (1)
25 (1)
30 (1)
Zbirovia
Zdicella
Thomastus
Cekovia
Octillaenus
Snajdria
Stenopareia
Alceste
Ligiscus
Ulugtella
Excetra
Ectillaenus
Rhaxeros
Cybantyx
Failleana
Platillaenus
Bumastus (Bumastus)
Bumastoides
Illaenus
Parillaenus
Bumastus (Bumastella)
Litotix
Paracybantyx
Liolalax
Nanillaenus
Thaleops
Ottenbyaspis
Panderia
Dysplanus
Zetillaenus
Harpillaenus
Dulanaspis
Lamproscutellum
Theamataspis
Waisfieldaspis
Eokosovopeltis
Kolihapeltis
Eobronteus
Planiscutellum
Paralejurus
Ancyropyge
Weberopeltis
Exastipyx
Xyoeax
Dentaloscutellum
Opoa
Calycoscutellum
Avascutellum
Kosovopeltis
Cavetia
Thysanopeltis
Scabriscutellum
Izarnia
Meridioscutellum
Metascutellum
Bojoscutellum
Decoroscutellum
Poroscutellum
Scutellum
Cornuscutellum
Spiniscutellum
Platyscutellum
Meroperix
Perischoclonus
Phillipsinella
Turgicephalus
Bronteopsis
Stygina
Raymondaspis
A
B
C
D
E
F
Illaenus
Kolihapeltis
Thysanopeltis
Scutellum

Figure 5.2: The MPT from the analysis that has the same branching pattern as the majority-rule tree (including other compatible groupings). Bootstrap values and branch support values (given in adjacent brackets where >0) are shown above the branches. Clades A–F are indicated. Green nodes delineate familial groupings, red nodes delineate subfamilial. The positioning of the line drawings does not relate directly to the clade the taxon is found in.

5.3 DISPARITY

5.3.1 METHODS

5.3.1.1 Taxon and character sampling

Please see section 4.3.1.1 for details.

5.3.1.2 Temporal sampling

See Section 4.3.1.2 for details. Temporal divisions are depicted in Figure 5.3.

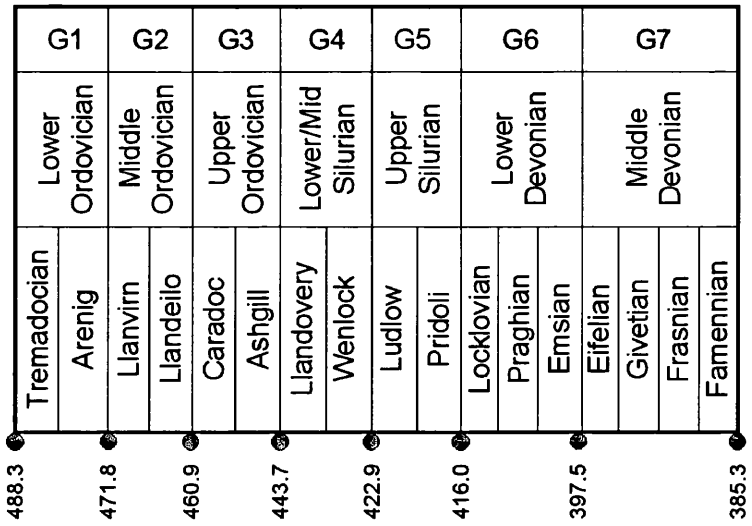

Figure 5.3: Temporal scale used in this study. Values indicate age of stage boundaries in Myr (from http://www.stratigraphy.org/geowhen/geolist.html). Intervals made of amalgamated stages used here (G1-G7) are shown on the top and geological stage in the centre (see Appendix IX for details of taxa assigned to time slices).

5.3.1.3 Euclidean distance analyses

The first analysis conducted was a Euclidean distance analysis on the raw dataset (Appendix VII) calculating the mean distance between all genera from a given time interval. See section 4.3.1.3 for coding method.

5.3.1.4 PCO

The MVSP data for these axes were read into RARE 1.1 (Wills 1998): this was used to calculate the sums and products of both the variance and range along the first 33 coordinate axes and allows comparison between samples of different sizes. This number of axes was used because they encompass 90% of the total variance.

5.3.2 RESULTS

5.3.2.1 Analysis by age: Euclidean distance analyses of PCO data

Distance from the outgroup for all ages range from 2.92 (e.g. *Turgicephalus*) to 5.13 (e.g. *Dentaloscutellum*). See Figure 5.4 for the arrangement of the organisms from the analysis.

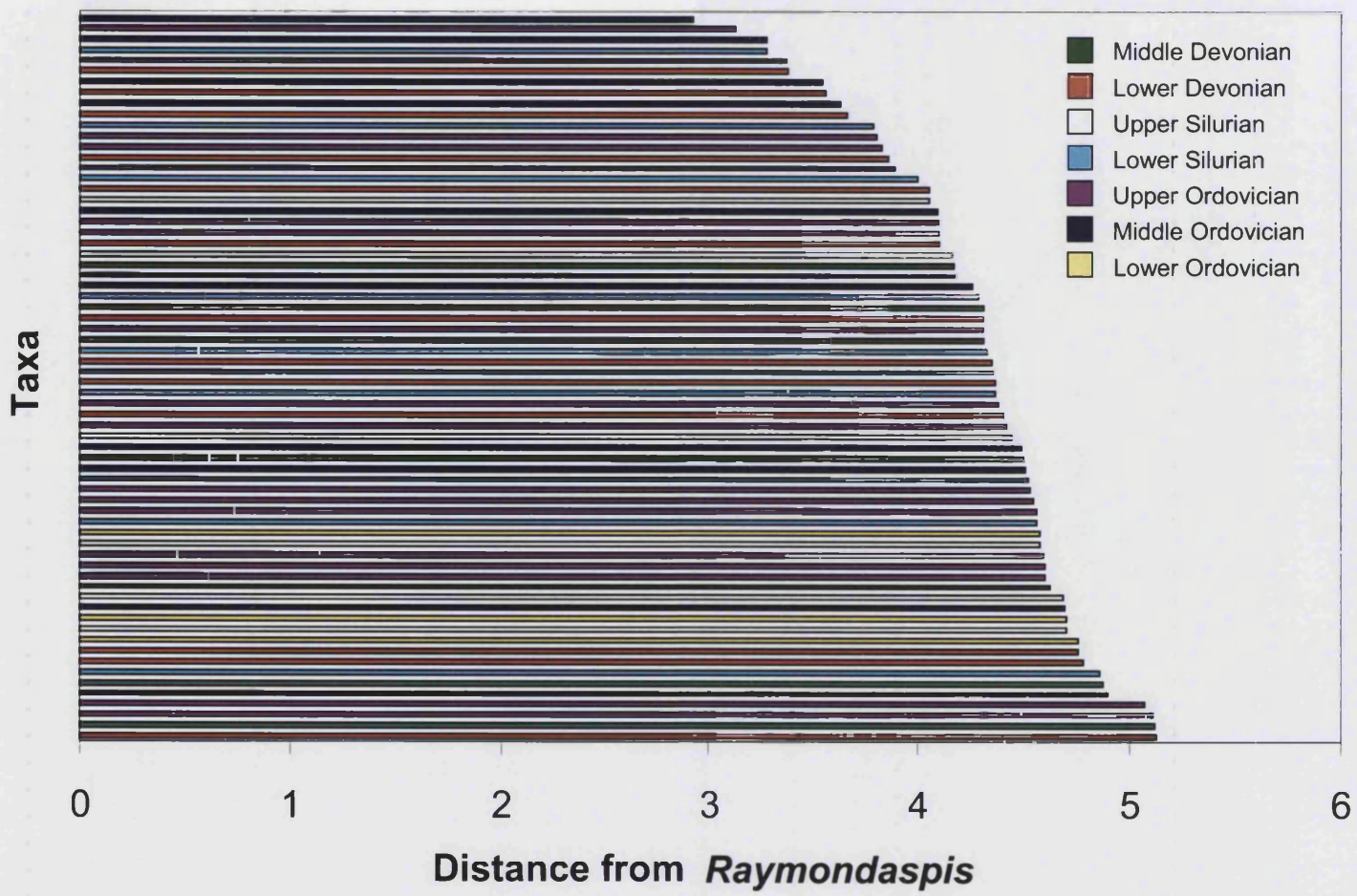

Figure 5.4: Results from Euclidean distance analysis of raw data. Each horizontal bar represents one taxon. Distance was calculated by using *Raymondaspis* as the outgroup. Taxon bars are coloured according to the time-slices specified.

5.3.1.2 *Analysis by age*

Taxa from all time slices seem evenly distributed and interspersed. Mean disparity shows a decreasing trend through time, with an unexpected increase before extinction in the Lower Devonian (see Figure 5.5).

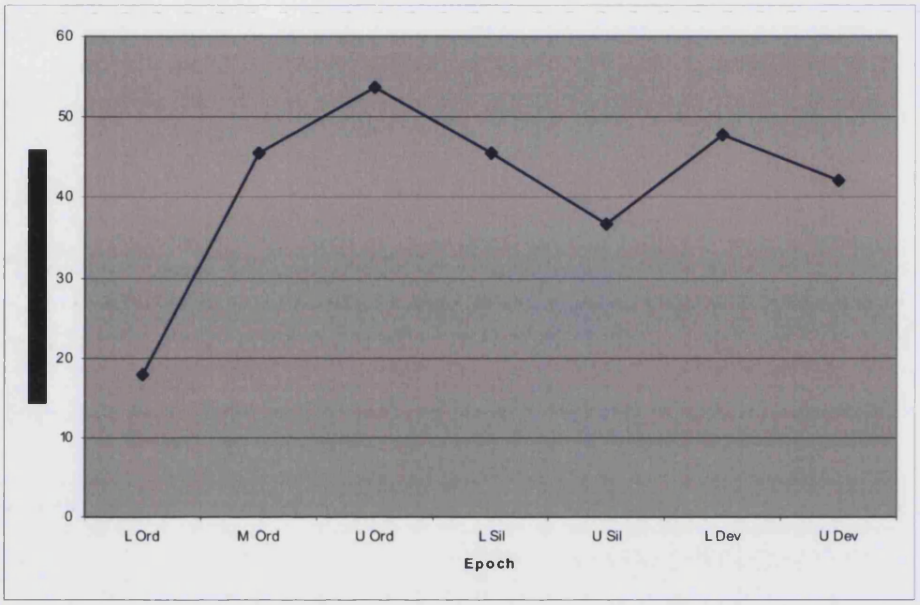

Figure 5.5: Mean disparity of illaenoid taxa through time (i.e. plotted mean end-point of curves from 5.6).

A test was conducted on the sum of ranges data for all time slices on all coordinate axes (see Appendix VIII for raw data) to see if the disparity of taxa at any given time was significantly different from random from a similar-sized sample drawn from the universe of all realized body-plans (Figure 5.6).

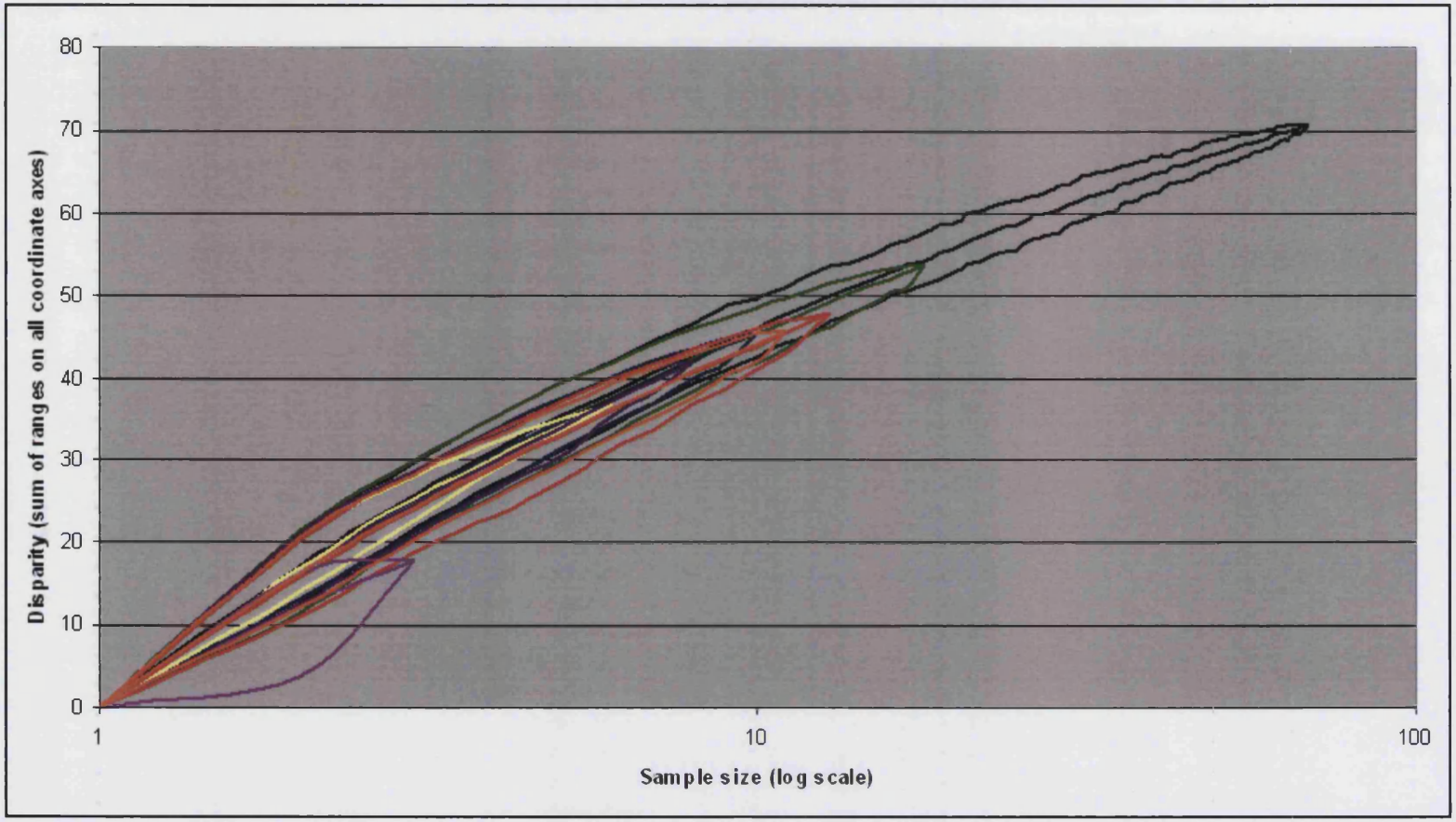

Figure 5.6: Rarefaction curves of measures of morphological disparity for illaenoid taxa in different time slices (sum of ranges data: 1000 random draws of taxa were made by randomising at each sample size, providing a mean value for the respective measure of morphological variety, along with upper and lower 90% confidence limits). Black = all taxa; pink = Lower Ordovician taxa; orange = Middle Ordovician; green = Upper Ordovician taxa; blue = Lower Silurian taxa ; yellow = Upper Silurian; red = Lower Devonian; purple = Upper Devonian.

Disparity values of taxa in all time slices are not significantly different when compared to entire dataset or each other (the rarefaction curves follow very similar trajectories and all mean values lie within the 90% confidence limits for the whole dataset and all time slices).

5.3.2.3 *Analysis by clade*

The clades display differing levels of mean disparity, with clades A and E having higher mean disparity than other illaenoid clades (Figure 5.7).

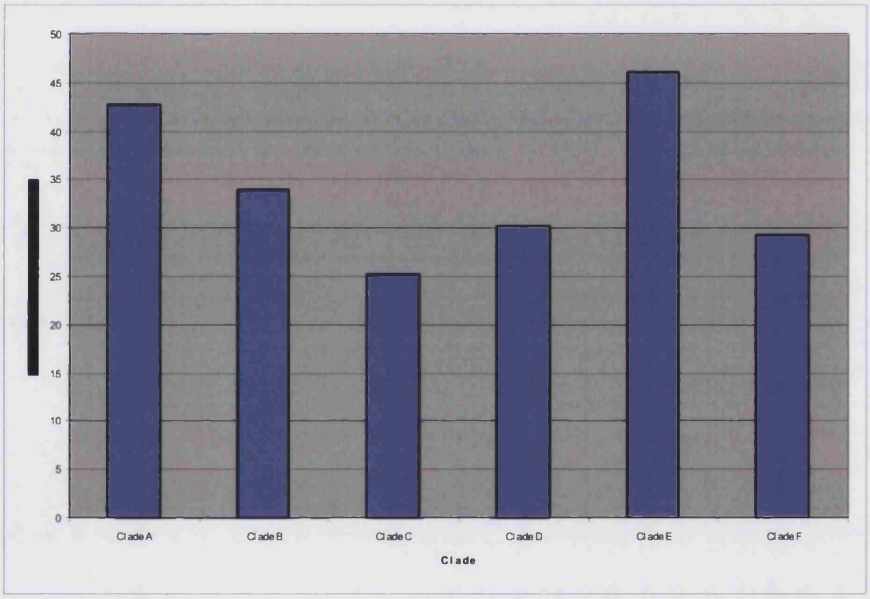

Figure 5.7: Mean disparity of clades of illaenoid taxa as a histogram (i.e. plotted mean end-point of curves from 5.8).

A test was conducted on the sum of ranges data for all clades on all coordinate axes (see Appendix VII for raw data) to see if the disparity of taxa for a clade was significantly different from random from a similar-sized sample drawn from the universe of all realized body-plans (Figure 5.8).

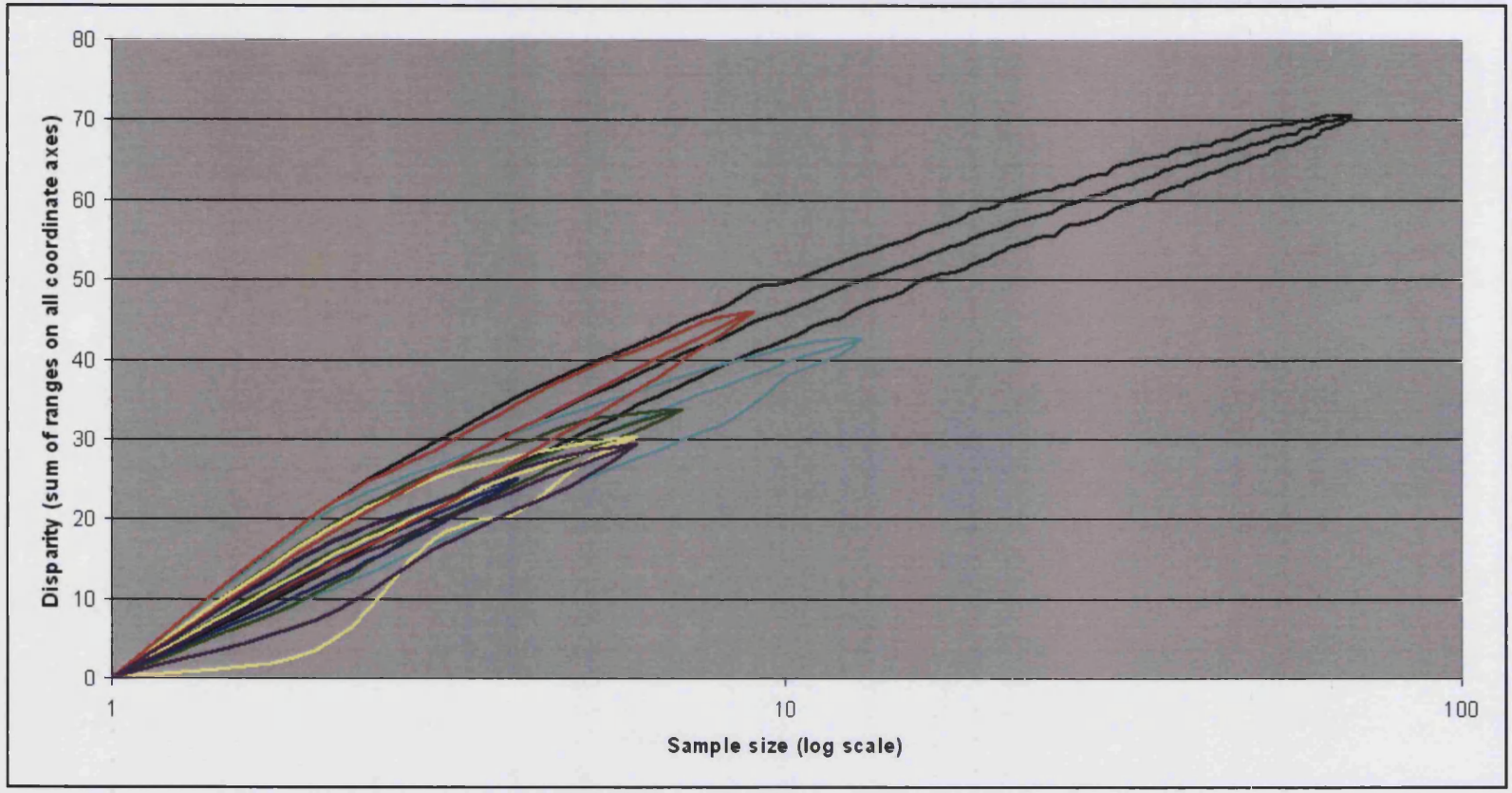

Figure 5.8: Rarefaction curves of measures of morphological disparity for different illaenoid clades (sum of ranges data: 1000 random draws of taxa were made by randomising at each sample size, providing a mean value for the respective measure of morphological variety, along with upper and lower 90% confidence limits). Black = all taxa; aqua = clade A; green = clade B; blue = clade C; yellow = clade D; red = clade E; purple = clade F.

Disparity values of different clades are significantly different when compared (Figure 5.8). Clade E (the Kosovopeltinae; see Section 5.5) has significantly higher disparity to all other clades (its mean values lie outside the 90% confidence limits of all other sampled clades; Figure 5.8).

5.3.2.4 *Principal Coordinates Analysis (PCO)*

Please see Section 4.3.2.4. Results for the first three PCO axes are plotted in a graph (Figure 5.9).

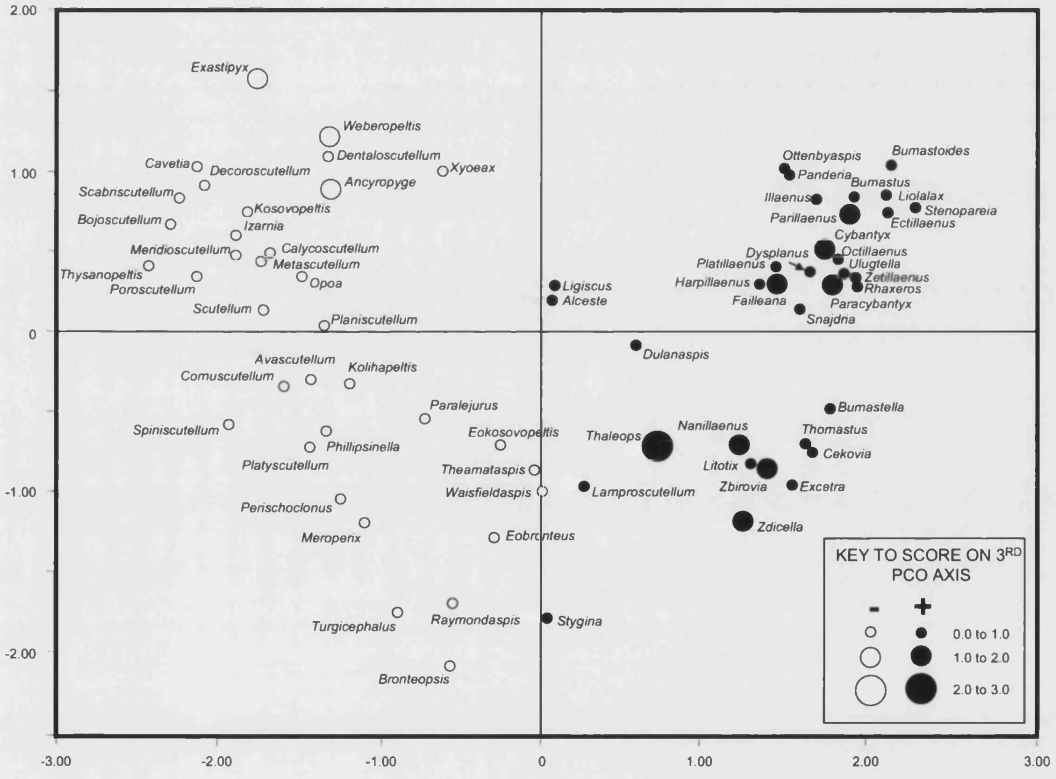

Figure 5.9: Mean disparity of illaenoid taxa. The 1st two PCO axes are shown as the axes of the graph and the third axis is indicated by size of the circles.

Analysis by age: Results for the first three PCO axes are plotted in a graph (Figure 5.10). Time slices plot in overlapping areas of morphospace defined by the first three principal coordinate axes. The time slices are indicated by coloured rings.

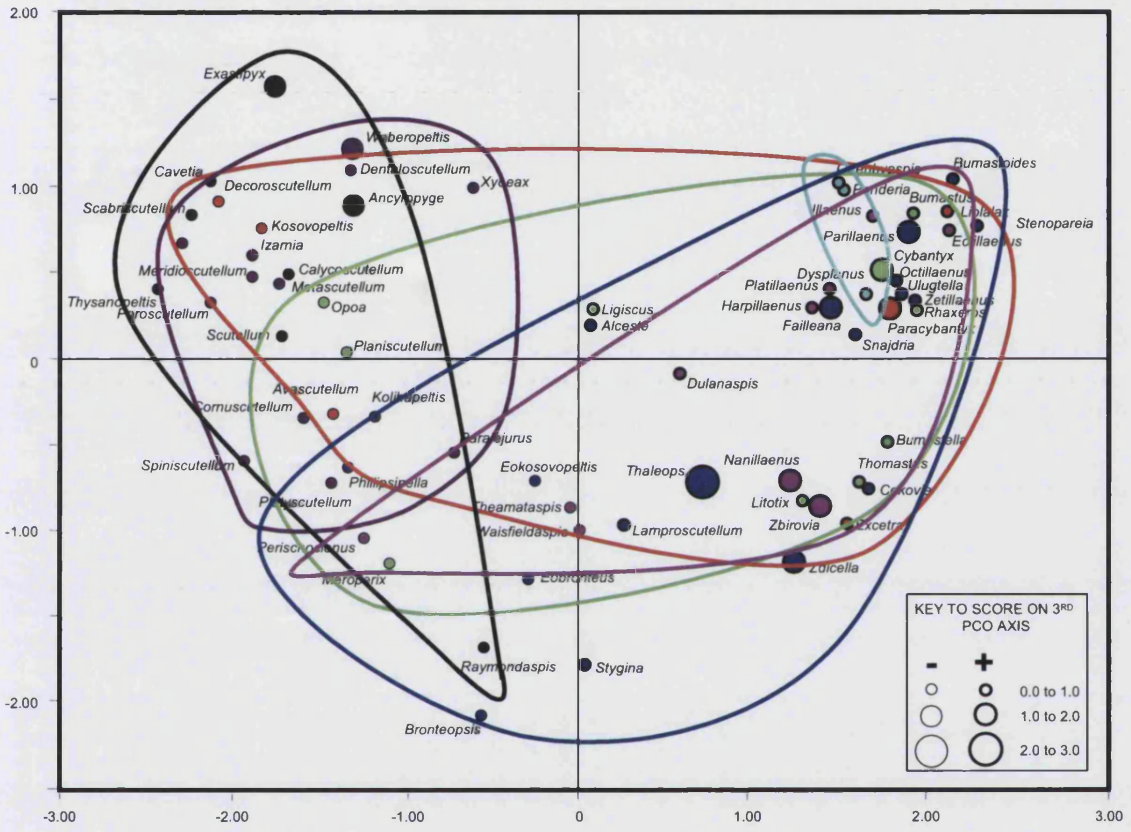

Figure 5.10: Distribution on the 1st three principal coordinates axes of all genera divided into age categories. The 1st two PCO axes are shown as the axes of the graph and the third axis is indicated by size of the circles. (Lower Ordovician = aqua; Middle Ordovician = lilac; Upper Ordovician = blue; Lower Silurian = lime green; Upper Silurian = red; Lower Devonian = purple; Middle Devonian = black).

Analyses by major taxonomic group: Results for the first three PCO axes are plotted in a graph (Figure 5.11). Major groups plot in distinct and generally non-overlapping areas of morphospace defined by the first three principal coordinate axes. The clades are indicated by coloured rings.

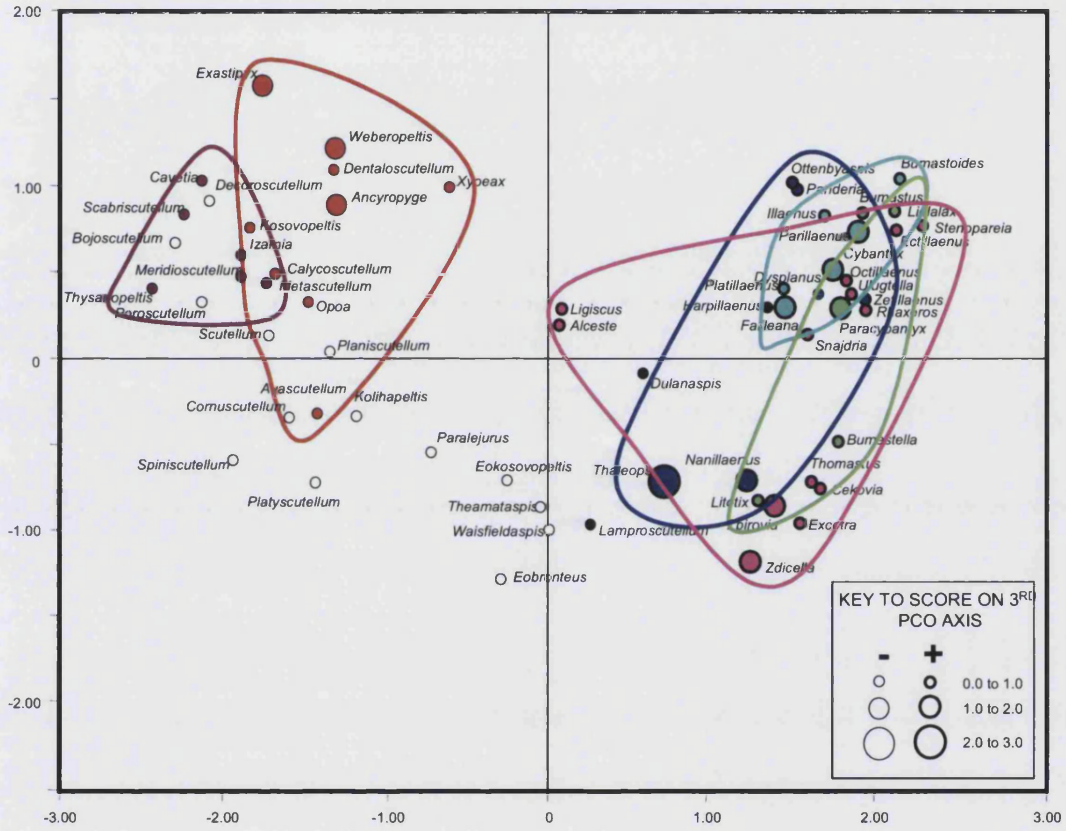

Figure 5.11: Distribution on the 1st three principal coordinates axes of all genera. The 1st two PCO axes are shown as the axes of the graph and the third axis is indicated by size of the circles. Taxa are identified by coloured circles as to their major taxonomic grouping. (Clade A = pink; clade B = aqua; clade C = lime green; clade D = blue; clade E = red; clade F = purple).

5.4 DISCUSSION

5.4.1 PHYLOGENETIC ANALYSIS (see *Systematic Palaeontology*, section 5.5)

5.4.2 DISPARITY

5.4.2.1 Disparity patterns over time

The Euclidean distance analyses on the raw data suggest that the mean disparity of earlier taxa is generally higher than later taxa (with a slight rise in the Upper Ordovician, a steady decline until the Upper Silurian and then a rise in the Lower Devonian; Figure 5.5). However, these differences are not statistically significant (Figure 5.6). Smith & Leiberman (1999) found a similar result with their study of the early Cambrian olenelloids.

The PCO analysis results show that the groupings are vastly overlapping. There does seem to be a shift of occupied morphospace over time: a clockwise rotation around the centre of the axes occurs (Figure 5.10).

5.4.2.2 Taxonomic disparity patterns

The clades display different measures of mean disparity (Figure 5.7). However, only the kosovopeltines have significantly different disparity to the other clades: the kosovopeltines display higher disparity than the other clades (Figure 5.8). This may be due to the Kosovopeltinae containing many highly spinose and unusual forms (e.g. *Xyoeax* and *Exastipyx*; see Holloway 1996).

Major clades from the resulting phylogeny seem to occupy discrete areas of morphospace when plotted along the three most important axes (but this is not statistically-significant; Figure 5.11) and some groups cluster more tightly than other groups (e.g. clade B *cf.* clade A).

5.5 SYSTEMATIC PALAEONTOLOGY

Suborder **ILLAENINA** (*sensu* Jaanusson, 1959 *in* Moore, 1959)
Superfamily **ILLAENOIDEA** Hawle & Corda, 1847

TAXA INCLUDED. Families Illaenidae (*sensu* Hupé, 1953) and Styginidae (*sensu* Skjeseth, 1955) plus *Meroperix* Lane, 1972, *Perischoclonus* Raymond, 1925, *Phillipsinella* Novák, 1885, *Turgicephalus* Fortey, 1980, *Bronteopsis* Etheridge & Nicholson *in* Nicholson & Etheridge, 1879, *Stygina* Salter, 1853 and *Raymondaspis* Whittington, 1965.

REMARKS. *Turgicephalus* is closely-related to, but separate from, *Raymondaspis (*as suggested by Fortey 1980). *Stygina*, *Bronteopsis*, *Perischoclonus* and *Raymondaspis* are all considered basal styginid taxa (Skjeseth 1955, Whittington 1963). Here those taxa appear basal to the illaenid and styginid taxa. *Phillipsinella* is considered closely-related to *Stygina* and *Bronteopsis* (in agreement with Reed 1931).

Bronteopsis should be excluded from the Styginidae (in agreement with the views of Whittington (1950) and Warburg (1925): *cf.* Skjeseth (1955) and Thorslund (1940)).

Phillipsinella Novák, 1885 was thought to have affinities with early scutelluid genera (Whittington 1950, p. 561; Bruton 1976, p. 704). It shares the following features with early scutelluids: (1) S2 connects to axial furrow (ch. 7); (2) lateral border furrow present on librigena (ch. 20); (3) eye lobe far back on cheek and close to axis (ch. 23); (4) relatively long pygidial axis (ch. 79) and (5) absence of medial flattened pygidial rib (ch. 81).

Family **ILLAENIDAE** (*sensu* Hupé, 1953) = illaenid

EMENDED DIAGNOSIS. Longitudinal glabellar furrow present (ch. 15*). Lateral border furrow on librigena absent (ch. 20*). Vincular fold present (ch. 22*). Eye lobe near posterior border (ch.23*). Posterior points of rostral plate are not dorsally bent (ch. 43*). Ten thoracic segments (ch. 48*). Medial rib present (ch. 81*). Pygidial axis present (ch. 87*).

TAXA INCLUDED. Subfamilies Ectillaeninae Jaanusson, 1959 *in* Moore 1959, Illaeninae Hawle & Corda, 1847, Bumastellinae Pollitt, 2006 and Panderiinae Bruton, 1968 plus *Dulanaspis* Chugaeva, 1956, *Eobronteus* Reed, 1928, *Eokosovopeltis* Jaanusson, 1953,

Harpillaenus Whittington, 1963, *Kolihapeltis* Prantl & Přibyl, 1947, *Lamproscutellum* Yin, 1980, *Paralejurus* Hawle & Corda, 1847, *Planiscutellum* Richter & Richter, 1956, *Theamataspis* Öpik, 1937 and *Waisfieldaspis* Vaccari, 2001.

STRATIGRAPHICAL RANGE. Early Ordovician to Upper Devonian (Frasnian).

REMARKS. *Eobronteus* and *Planiscutellum* share 'several special evolutionary primitive features' (Šnajdr 1960, p. 240). *Theamataspis* should neither be assigned to its own subfamily (*cf.* Hupé 1953), nor to the Styginidae (*cf.* Lane 1972, p. 340) but should be considered to be more closely-related to the Illaenidae. It does display an amalgam of illaenid and styginid characters (see Fortey 1980, p. 57) but should be regarded as a basal illaenid. *Dulanaspis* is closely-related to *Theamataspis* (as suggested by Fortey 1980) but the paraphyletic position of the former taxon within the Illaenidae suggests that the subfamily Dulanaspinae Přibyl & Vaněk, 1971 is superfluous.

Waisfieldaspis is not a styginid (*cf.* Vaccari 2001) but is an illaenid and is closely-related to *Ancyropyge* (in concordance with Ormiston 1967). *Eokosovopeltis* and *Lamproscutellum* share a close phylogenetic relationship (as suggested by Edgecombe *et al.* 2004).

Effacement is commonplace in this group. Lane & Thomas (1983) suggested there are two groups: (1) *Illaenus*, *Bumastoides*, *Stenopareia* and *Thaleops* and taxa generally referred to the Ectillaeninae; and (2) 'effaced styginids' (see below). The former group does not cluster neatly in this study: although *Illaenus*, *Bumastoides* and the Ectillaeninae are closely-related.

The latter group was thought to comprise several genera (previously assigned to the Illaenidae) that should be re-assigned to the Scutelluidae as 'effaced styginids' or 'illaenomorph' taxa (=Styginidae; Lane & Thomas 1978, 1983). These illaenomorph taxa were: *Alceste*, *Bumastus*, *Cybantyx*, *Dysplanus*, *Failleana*, *Kosovopeltis*, *Liolalax*, *Litotix*, *Planiscutellum*, *Platillaenus* and *Rhaexeros*. Proposed illaenomorph character states *cf.* with those of true illaenids are: (1) larger eyes (ch. 24); (2) glabella is more expanded (tr.) anteriorly (ch. 30); (3) presence of anterior pit (ch. 32); (4) cephalon is less convex (lower than long in lateral view; ch. 38); (5) axis and articulating free portions of thoracic pleurae are not demarcated (ch. 58); (6) pygidium is equal/longer in relation to cephalon (ch. 62); (7) lacks pygidial doublure projections (ch. 71); (8) weak pygidal axial furrows (ch. 78) and (9) pygidial post-axial ridge (ch. 80).

	Alceste	*Bumastus*	*Cybantyx*	*Dysplanus*	*Failleana*	*Kosovopeltis*	*Liolalax*	*Litotix*	*Planiscutellum*	*Platillaenus*	*Rhaxeros*	Proportion
Ch. 24	-	+	+	-	+	+	+	+	-	+	-	7/11
Ch. 30	-	+	+	+	+	+	?	+	+	+	-	8/11
Ch. 32	-	-	+	+	+	-	+	+	-	+	-	6/11
Ch. 38	-	-	-	-	+	-	-	-	+	-	-	2/11
Ch. 58	?	?	+	-	+	-	+	?	-	?	-	3/11
Ch. 62	-	+	+	-	-	+	+	+	+	+	+	8/11
Ch. 71	?	+	+	+	+	+	+	?	?	+	?	8/11
Ch. 78	-	+	+	+	+	-	+	+	-	+	+	8/11
Ch. 80	-	+	+	-	-	-	-	+	-	-	-	3/11
Proportion	0/9	6/9	8/9	4/9	7/9	4/9	6/9	6/9	3/9	6/9	2/9	

Table 5.3: Correlations of illaenomorphic characters and proposed illaenomorph taxa from Lane & Thomas (1978, 1983). (+ve symbol = illaenomorph character state present; -ve symbol = illaenomorph character state absent.)

This study does not support the division between illaenids and effaced styginids and, instead, places all illaenomorph taxa, bar *Kosovopeltis*, within the Illaenidae. *Alceste* possesses none of the proposed illaenomorphic character states listed above (where known; coded from literature referenced in table 5.1), *Rhaexeros* possesses only two, and *Planiscutellum* only three (Table 5.3). *Dysplanus* and *Kosovopeltis* display four, *Bumastus*, *Liolalax*, *Litotix* and *Platillaenus* six and *Failleana* and *Cybantyx* seven and eight respectively.

These illaenomorph taxa do not form a monophyletic clade (in agreement with Lane & Thomas 1983). *Kosovopeltis* is a scutelluid, *Planiscutellum* is a basal illaenid but the other illaenomorphs are all distributed between the illaenid subfamilies Ectillaeninae, Illaeninae and Bumastellinae (see below).

Some of the characters are shared by more illaenomorph taxa than others (e.g. ch. 30 *cf.* ch. 38). Some of the character states are shared with styginids, e.g. character 30 but some are shared with the illaenids as well (chs 58 and 78).

The illaenomorph character states may be influential (four of the illaenomorphs group together in the Illaeninae). However, the illaenomorphic character states shared by many illaenomorph taxa are not exclusive and many of them are homoplasious and shared with many styginid *and* illaenid taxa. Perhaps these character states should be viewed as states that seperate most of the illaenomorph taxa from the Ectillaeninae but do not add enough weight to cancel out those that group them with the Illaenidae.

Subfamily **ECTILLAENINAE** Jaanusson, 1959 *in* Moore, 1959

EMENDED DIAGNOSIS. Small eyes or blind (ch. 24). Narrow anterior wings of hypostome (ch. 45). No discrete half-ring present (ch. 53*).

TAXA INCLUDED. *Alceste* Hawle & Corda, 1847; *Cekovia* Šnajdr, 1956; *Ectillaenus* Salter, 1867; *Excetra* Holloway & Lane, 1998; *Ligiscus* Lane & Owens, 1982; *Octillaenus* Salter, 1867; *Rhaxeros* Lane & Thomas, 1980; *Snajdria* Hammann, 1992; *Stenopareia* Owen & Bruton, 1980; *Thomastus* Öpik, 1953; *Ulugtella* Petrunina *in* Repina *et al.*, 1975; *Zbirovia* Šnajdr, 1956; *Zdicella* Šnajdr 1957.

STRATIGRAPHICAL RANGE. Middle Ordovician to Upper Silurian.

REMARKS. *Cekovia* differs from other illaenids in having: a strongly swollen cephalon and glabella, distinct and long axial furrows, eyes situated posteriorly, 10 thoracic segments and pygidium with semicircular posterior margin (Bruthansová 2002). According to this study, *Cekovia* is placed within the Illaenidae: the similarity of the juveniles to *Raymondaspis* is due to convergence (Hammann 1992, p. 49) and, hence, not reason alone to place them in Styginidae.

According to this study *Octillaenus* has not developed paedomorphically from *Parillaenus* (*cf.* Bruton & Owens 1988; Bruthansová 2003, p. 176).

It has been thought that *Zbirovia*, *Alceste*, *Zdicella*, *Zbirovia* and *Ulugtella* can only be distinguished on the basis of their pygidia (Bruthansová 2003): this study disputes that. *Zbirovia* has no eyes, outwardly curved and short axial furrows, semicircular cephalic outline, 10 thoracic segments, trapezoidal outline and large doublure. It differs from *Alceste* by: shorter, less distinct and more outwardly curved axial furrows, trapezoidal outline of pygidium. It differs from *Zdicella* by its slightly downwardly-curved fixigena, rather than straight. *Alceste* is considered to belong to the Illaenidae rather than the Styginidae *sensu* Lane & Thomas (1983), in agreement with Hammann (1992, p. 72). *Snajdria* is closely-related to *Zdicella* in agreement with Hammann (1992, p. 78).

Blindness has evolved at least twice: *Zbirovia+Zdicella* and *Ulugtella+Alceste* have arisen from different stocks.

Ectillaenus has been thought to be closely-related to *Illaenus* (Salter 1867), *Parillaenus* Jaanusson, 1953 (Bruthansová 2003, p. 173) or *Zbirovia* (Bruthansová 2003, p. 175) but this analysis places it closely-related to *Excetra*.

That *Ulugtella* is a junior synonym of *Stenopareia* (Hammann 1992, Bruthansová 2003) or *Zbirovia* (Hammann 1992, p. 75) is not supported here. Neither is it thought here to be very closely-related to *Zdicella* or *Zbirovia* (see Hammann 1992).

Excetra resembles *Ligiscus* (for discussion, see Holloway & Lane 1998, p. 873).

Zetillaenus is closely-related to *Dysplanus* (in agreement with Hammann 1992, p. 52).

Subfamily **ILLAENINAE** Hawle & Corda, 1847

EMENDED DIAGNOSIS. Scattered pit between terrace ridges (ch. 1*). Weak median glabellar node (ch. 31). Rostral flange present (ch. 42*). Long axial thoracic ring (ch. 49*). Long doublure of axial ring (ch. 51). No genal spine at meraspid stage (ch. 93*).

TAXA INCLUDED. *Bumastus* Murchison, 1839; *Bumastoides* Whittington, 1954; *Cybantyx* Lane & Thomas *in* Thomas, 1978; *Failleana* Chatterton & Ludvigsen, 1976; *Illaenus* Dalman, 1827; *Parillaenus* Jaanusson, 1953; *Platillaenus* Jaanusson, 1953.

STRATIGRAPHICAL RANGE. Early Ordovician to Lower Silurian.

REMARKS. This study suggests that *Cybantx* is an illaenid (in agreement with Whittington 1997, see above for fuller explanation). It is closely-related to *Bumastus* (as suggested by Lane & Thomas 1978).

Failleana is closely-related to *Platillaenus* (Lane & Thomas 1983). Here it is thought to be an illaenid (as suggested by Whittington 1997).

Parillaenus may be a subgenus with *Illaenus* (as suggested by many authors, e.g. Dean 1978; Owen & Bruton 1980) but they differ in various aspects. *Parillaenus* has an: anterior pit; a flap-like librigenal spine rather than the reduced spines of *Illaenus*; 7 thoracic segments rather than the 10 of *Illaenus*; posteriorly divergent thoracic axial furrows rather than convergent; wide pygidium; no forward projection on pygidial doublure rather than the simple one of *Illaenus*; an undifferentiated pygidial axis and a narrow pygidial axis relative to its entire width.

Bumastoides is regarded as an illaenine (see also Ludvigsen & Chatterton 1980). *Bumastus* and *Bumastella* have been given generic-status as they do not group within the same subfamily.

Subfamily **BUMASTELLINAE** Pollitt *et al.*, 2006

EMENDED DIAGNOSIS. Medium eye size (ch. 24*). Anterior pit present (ch. 32, excluding *Bumastella*). Anterior node present (ch. 33). Rounded genal librigena (ch. 35*). Half-rings present (ch. 53*). Anterior margin of pygidium delimits pygidium almost to a circle (ch. 85*). Absence of spines of transitory pygidium (ch. 96*). Absence of inter-ring furrows on early pygidia (ch. 97).

TAXA INCLUDED. *Bumastella* Kobayashi & Hamada, 1974; *Liolalax* Holloway & Lane 1999; *Litotix* Lane & Thomas *in* Thomas, 1978; *Paracybantyx* Ludvigsen & Tripp, 1990.

STRATIGRAPHICAL RANGE. Lower Silurian to Upper Silurian.

REMARKS. *Bumastella* was originally erected as a subgenus of *Bumastus* (Kobayashi & Hamada 1974, p. 50) but it is now considered to have little similarity to the latter genus (Holloway & Lane 1998, p. 866) – a view that is supported here.

Litotix resembles *Liolalax* (Holloway & Lane 1998, p. 877): a view maintained in this study. The meraspid transitory pygidia of *Liolalax* and *Bumastella* are exceedingly similar (Holloway & Lane 1998, p. 883). These taxa are closely-related.

The new subfamily Bumastellinae Pollitt, 2006 is erected. Bumastinae Raymond, 1916 has become a junior subjective synonym of Illaeninae Raymond, 1916 and cannot be used as a seperate subfamily.

Subfamily **PANDERIINAE** Bruton, 1968

EMENDED DIAGNOSIS. Thoracic articulating furrow absent (ch. 50*). Axial rings of thorax are flattened (ch. 52*). Convergent thoracic axial furrows (ch. 57). Deep thoracic axial furrows (ch. 58). Thoracic axis is ≥1/3 of entire thoracic width (ch. 59*). Pygidium smaller than cranidium (ch. 62). Pygidial axis is ≥1/3 of anterior pygidial width (ch. 84*).

TAXA INCLUDED. *Dysplanus* Burmeister, 1843; *Nanillaenus* Chatterton, 1980; *Ottenbyaspis* Bruton, 1968; *Panderia* Volborth, 1863; *Thaleops* Conrad, 1843; *Zetillaenus* Šnajdr, 1957.

STRATIGRAPHICAL RANGE. Lower Ordovician to Upper Ordovician.

REMARKS. *Panderia* and *Ottenbyaspis* are closely-related to the Illaenidae as suggested by Bruton (1968). *Nanillaenus* and *Thaleops* are closely related to them. They share a closer relationship with the Bumastellinae than the Illaeninae (the presence of the triangular rostal flange shared with *Stenopareia* is insignificant).

Thaleops Conrad, 1843 is closely related to *Nanillaenus* Jaanusson, 1953 (Chatterton & Ludvigsen 1976; Amati & Westrop 2004).

Dysplanus Burmeister, 1843 and *Zetillaenus* Šnajdr, 1957 may be synonymous (but see Bruthansová 2003, p. 177). They appear as sister-groups here, but differ in the several aspects. *Dysplanus* has: scattered pits between terrace ridges on exoskeleton rather than fine pitting; a lateral border furrow on librigena; great anterior expansion rather than slight; an anterior pit; radiating ribs on the pygidium and an extensive pygidial doublure rather than a narrow one. *Dysplanus* is not a styginid (*cf.* Hammann 1992, p. 52).

Family **STYGINIDAE** (*sensu* Skjeseth, 1955) = styginid

EMENDED DIAGNOSIS. Fine pitting over cranidium surface (ch. 1*). S1 bifurcate with strong, small median node (ch. 12*). L2-L3 inflated (ch. 14*). Longitudinal glabellar furrow present (ch.15*). Lateral border furrow absent (ch. 20*). Vincular fold present (ch. 22*). Eye lobe near posterior border (ch. 23*). Eye ridges present (ch. 28). Occipital tubercle absent (ch. 40*). Posterior points of rostal plate dorsally bent (ch. 43*). Short posterior lobe of hypostome (ch. 44*). Large anterior wings of hypostome (ch. 45*). 10 thoracic segments (ch. 48*). Pygidial axis divided into 3 portions (ch. 87*). Pleural furrow of transitory pygidium absent (ch. 90*). Node present on palpebral lobes (ch. 92*). Long occipital spine that shortens throughout ontogeny (ch. 94*). Axial spines present on all meraspid pygidial segments (ch. 98*). Distinctive tuberculation pattern at early meraspid stage (ch. 99*).

TAXA INCLUDED. Subfamilies Kosovopeltinae Pollitt, 2006 and Thysanopeltinae Hawle & Corda, 1847 plus *Bojoscutellum* Šnajdr 1958, *Cornuscutellum* Šnajdr 1960, *Decoroscutellum* Šnajdr 1960, *Platyscutellum* Šnajdr 1958, *Poroscutellum* Šnajdr 1958, *Scutellum* Pusch 1833 and *Spiniscutellum* Šnajdr 1960.

STRATIGRAPHICAL RANGE. Lower Silurian to Middle Devonian.

REMARKS. Šnajdr (1960, p. 241) supposes that *Bojoscutellum* and *Cornuscutellum* are 'probably the last evolutional [*sic*] links of the line beginning with the genus *Decoroscutellum* Šnajdr'. This work suggest the opposite – that the last taxon arose from the stock containing first two, rather than them arising from *Decoroscutellum.*

Bojoscutellum, *Cornuscutellum*, *Decoroscutellum*, *Platyscutellum*, *Poroscutellum*, *Scutellum* and *Spiniscutellum* are thought to be closely-related (Šnajdr 1960, p. 241). Here they present as stem-group styginids.

The close relationship of thysanopeltids to the styginids (as supported by Lane & Thomas (1983)) is supported here.

Subfamily **KOSOVOPELTINAE** Pollitt *et al.*, 2006

EMENDED DIAGNOSIS. L2-L3 not inflated (ch. 14*). Subparallel anterior sutures (ch. 36). Median pygidial rib not bifid (ch. 82*).

TAXA INCLUDED. *Ancyropyge* Clarke, 1892; *Avascutellum* Šnajdr, 1989; *Calvcoscutellum* Archinal, 1994; *Dentaloscutellum* Chatterton, 1971; *Exastipyx* Holloway, 1996; *Kosovopeltis* Šnajdr, 1958; *Opoa* Lane, 1972; *Weberopeltis* Maksimova *in* Moore, 1959; *Xyoeax* Holloway, 1996.

STRATIGRAPHICAL RANGE. Lower Silurian to Middle Devonian.

REMARKS. *Ancyropyge*, *Xyoeax* and *Weberopeltis* are considered closely-related (in agreement with Holloway 1996, p. 433). Species of *Exastipyx* have commonly been assigned to *Weberopeltis* in the past (e.g. Feist 1974) and a close phylogenetic relationship is seen here (but Holloway considers the pygidial similarity to be convergently attained due to minor differences in cranidial morphology (1996, p. 437)).

The styginid connections of *Opoa* are confirmed (in agreement with Lane 1972). The subfamilial name Stygininae Vogdes, 1890 would not be appropriate here as the grouping does not contain *Stygina* Salter, 1853.

Subfamily **THYSANOPELTINAE** Hawle & Corda, 1847

EMENDED DIAGNOSIS. Median node is quite large and bears external sculpture (ch. 13); occipital tubercle present as stout spine (ch. 39*).

TAXA INCLUDED. *Cavetia* Feist, 1974; *Izarnia* Feist, 1974; *Meridioscutellum* Feist, 1970; *Metascutellum* Šnajdr, 1960; *Scabriscutellum* Richter & Richter, 1956; *Thysanopeltis* Hawle & Corda, 1847.

STRATIGRAPHICAL RANGE. Lower Silurian to Middle Devonian.

REMARKS. A close relationship between *Scabriscutellum* R. & E. Richter and *Thysanopeltis* Hawle & Corda, 1947 is seen here, as suggested by Šnajdr (1960). But,

Kolihapeltis Prantl & Přibyl is not closely-related to this group and is, indeed, not even included within the scutelluid clade (*cf.* Šnajdr 1960).

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6. Suggestions for further work

IN order to improve our knowledge of, and perhaps ultimately hold a definitive understanding of, trilobite phylogeny it is recommended that workers adopt certain additions or modifications when conducting similar studies in the future:

(1) Not all scorings by previous workers could be personally verified. A future analysis would try to check some of the more subtle character states from actual specimens rather than relying on the literature.

(2) Some states were constructed that measured the length/extent of structures. These structures were measured relative to another, but often required the conversion of continuous data into discrete states. These data could be further explored using morphometric techniques to see if there were 'natural' division in the expression of the state (e.g. Rae 1998[1]).

(3) A superior study of disparity would measure the stratigraphic ranges of taxa rather than treat the taxa as points in time (as was done here). The adoption of the quicker latter approach was necessary here: but it prevented much being said about the origin/extinction of a group and how much any group in particular contributed to the changes in disparity level.

(4) Sampling issues aside, there appeared to be a consistent expression of disparity within the illaenoids over time. This may be a true phenomenon, but there may be other influencing factors: perhaps the taxa coded did not show a representative pattern, and a pattern is seen more clearly in higher levels within some taxa. If so, an expanded study may show variations in disparity through time.

(5) Whittington rejected the close relationship between the illaenids and styginids and suggested that *Nileus* and allied genera (Nileidae) should be grouped together with the Illaenidae (2000[2]; *cf.* Fortey & Chatterton 1988[3] who placed the nileids in the Asaphidae). He based this proposal mainly on the absence of an articulating furrow in the thoracic rings of *Nileus* and the Illaenidae, and other characters that are associated mainly with effacement. Although it is thought here to be unlikely that Nileidae and Illaenidae are closely-related, it would be interesting to code some nileids into the dataset of Chapter 5 and explore this idea.

[1] **Rae, T. C.** 1998. The logical basis for the use of continuous characters in phylogenetic systematics. *Cladistics* **14:** 221–228.
[2] **Whittington, H. B.** 2000. Stygina, Eobronteus (Ordovician Styginidae, Trilobita): morphology, classification, and affinities of Illaenidae. *Journal of Paleontology* **74**: 879-889.
[3] **Fortey, R. A. & Chatterton, B. D. E.** 1988. Classification of the trilobite suborder Asaphida. *Palaeontology* **31**: 165-222.

7. Conclusions

ALTHOUGH trilobites have been mentioned in the scientific literature for some 200 years their evolutionary relationships are still contentious. Studies resolving this issue are necessary in order to assemble a stable trilobite classification and also to facilitate future macroevolutionary studies on the group.

This work investigated the phylogenies of four large trilobite groups: Lichoidea, Calymenina, Odontopleurinae and Illaenoidea. These four taxa have distinctive gross morphologies and present different challenges. Fine resolution was attained in all resulting phylogenies, the systematic palaeontology of each group was reassessed accordingly and phylogenetically valuable character states were noted.

A Bayesian phylogenetic method was employed on the lichoids. The trees obtained were similar to those inferred using parsimony, with the exception of relationships between the deeper branches and the groupings adhered well to those suggested in previous works.

Chapters 4 and 5 investigated the phylogeny of two large groups (odontopleurids and illaenoids respectively) and used the same character data to explore the *disparity* (morphological variety) of both groups. The disparity of odontopleurids decreased significantly through time, but that of illaenoids did not. The relative disparity of major clades within each group was also investigated. The Odontopleurinae has statistically significantly higher disparity compared to the Acidaspidinae (but equal to all others; see Chapter 4) and the particularly spiny Kosovopeltinae has significantly higher disparity to all other illaenoid clades (Chapter 5).

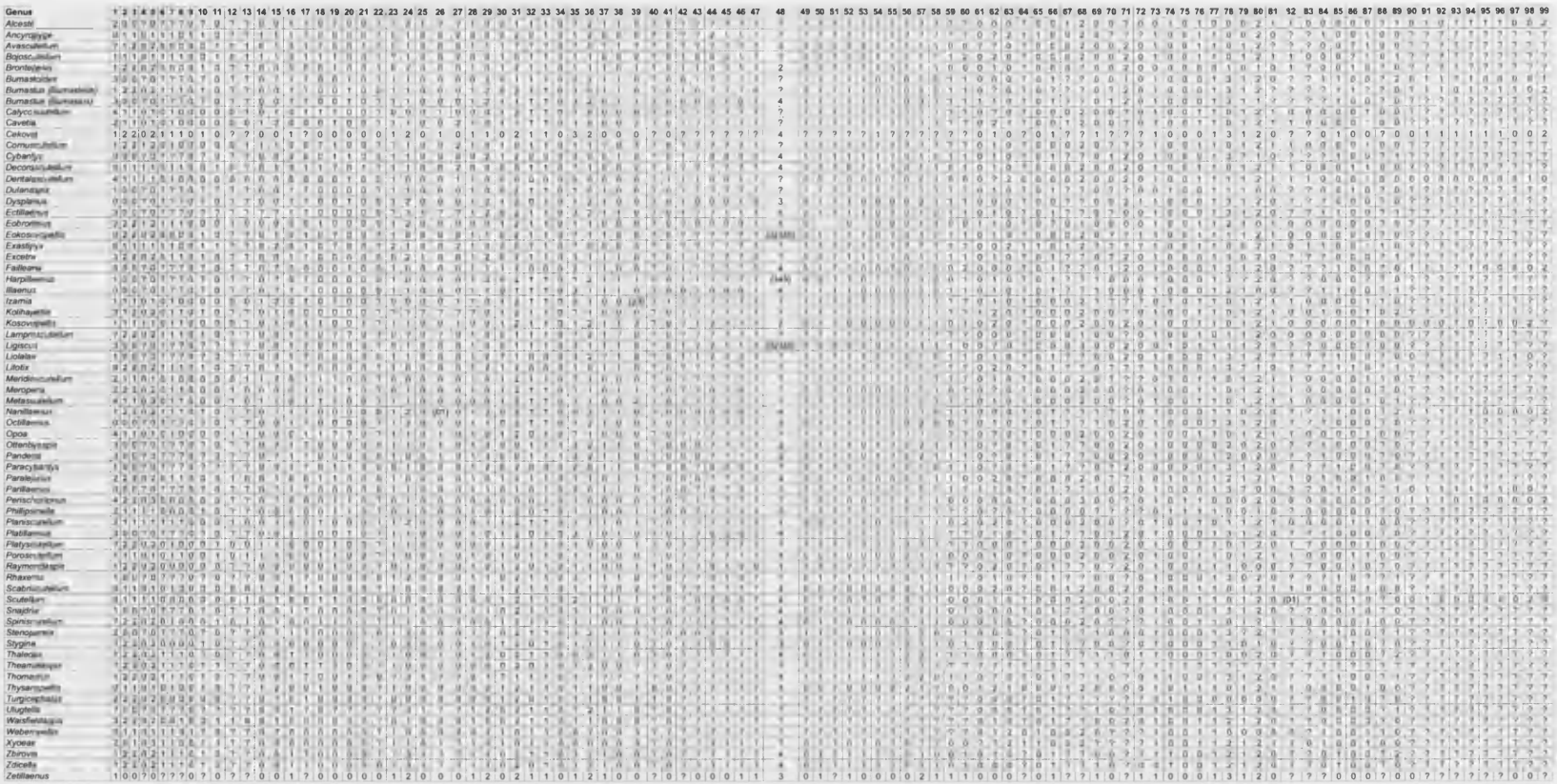
New subfamilies were erected in Chapter 4 (Subfamily Miraspinae Pollitt *et al.,* 2006) and 5 (Subfamilies Bumastellinae Pollitt *et al.*, 2006 and Kosovopeltinae Pollitt *et al.*, 2006) to encompass new groupings of taxa.

It is hoped that this work provides a platform for future trilobite workers: as this work utilised the invaluable literature of previous workers. This work will provide types of pitfalls that it is necessary to avoid and examples of robust characters to be taken into account for study of other trilobite groups.

8. Appendices

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	5
Alcymene neointermedia	?	?	0	0	1	1	2	0	1	1	2	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	2	1	0	0	1	0	1	0	1	0	0	?	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	1	
Apocalymene coppinsensis	?	?	0	0	1	1	2	0	1	1	2	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	2	0	2	1	0	0	0	0	1	0	0	0	0	?	0	0	1	0	0	1	0	1	0	0	0	1	0	1	?	?	1	
Arcticalymene viciousi	?	?	2	0	1	1	2	0	1	1	0	0	0	1	1	1	0	0	2	1	1	0	1	0	0	0	2	0	1	1	0	0	1	0	1	1	1	0	0	?	0	0	0	0	0	1	0	1	0	0	0	1	1	1	?	?	1	
Arduennella maxillieuxi	?	?	1	2	2	2	1	0	2	0	4	0	?	1	0	?	?	1	?	0	0	?	1	3	0	2	1	0	0	1	1	0	0	?	2	?	2	0	2	?	1	4	?	?	1	1	1	0	1	1	0	1	0	0	?	?	?	?	1	
Bathycheilus castilianus	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	1	2	1	1	1	1	0	0	0	0	2	?	2	1	?	0	1	1	2	?	1	0	1	1	0	0	0	1	0	1	1	?	0	
Bavarilla hofensis	0	0	0	1	0	1	1	0	2	0	1	0	0	2	0	0	1	1	?	0	0	1	0	1	0	?	2	1	2	0	1	0	0	0	2	?	2	0	2	?	0	1	?	?	?	?	0	1	0	1	0	1	0	1	0	0	0	
Brongniartella bisulcatus	?	?	?	1	(12)	0	1	0	2	1	3	?	?	?	?	?	?	?	?	0	0	?	0	0	0	0	?	?	0	0	1	0	0	0	2	?	2	0	2	?	0	0	2	?	?	?	0	0	0	0	0	1	0	1	0	0	0	
Burmeisterella armata	0	1	1	4	1	2	1	0	2	1	1	0	0	1	0	0	1	1	?	0	0	1	1	2	0	2	1	0	0	1	1	0	0	0	2	?	2	0	2	?	0	4	0	?	1	1	1	0	0	0	0	?	0	0	0	0	0	
Calymene blumenbachii	0	0	0	0	1	1	2	0	1	1	0	0	0	1	1	1	0	0	2	1	0	0	1	0	0	0	1	0	2	1	0	0	1	0	1	0	1	0	0	?	0	0	0	0	0	1	1	0	0	1	0	0	1	1		
Calymenella boisseli	?	?	0	3	1	1	1	0	2	2	1	0	0	2	0	0	1	0	0	0	0	1	1	0	1	1	2	0	2	0	0	0	0	0	2	?	2	1	?	0	0	1	1	?	1	0	1	0	?	0	0	0	0	1	?	?	1	
Calymenesun tingi	1	0	0	1	2	0	0	0	1	1	2	0	0	1	1	0	1	0	0	0	0	1	1	0	1	3	2	0	1	0	0	1	1	0	2	?	2	1	?	0	1	2	2	?	1	?	1	0	0	0	0	1	0	1	0	1	1	
Calymenia whittingtoni	?	?	?	?	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	0	3	2	0	2	0	0	0	0	0	0	0	2	1	?	0	0	1	1	?	0	0	?	1	?	?	?	0	?	?	?	1	?	?	
Colpocoryphe rouaulti	0	0	0	1	1	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	1	3	2	0	1	0	1	0	1	0	1	0	2	0	2	?	0	0	0	?	1	?	1	2	0	0	0	0	1	0	1	1	
Dekalymene crassa	?	?	?	?	1	1	1	2	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	?	1	0	0	1	0	?	?	1	0	1	?	0	?	?	1	0	1	1	0	?	?	?	?	?	?	?	?	
Diacalymene drummuckensis	0	0	0	1	1	1	2	0	1	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	1	?	0	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	1	
Digonus gigas	0	1	2	1	1	2	1	0	2	1	3	?	?	?	?	?	?	?	?	0	0	?	0	0	0	2	?	?	0	1	1	0	0	0	1	0	2	0	2	?	0	4	2	?	2	1	0	0	?	0	0	1	0	0	0	0	1	
Dipleura laevicauda	0	0	0	1	2	1	1	0	2	0	3	?	?	?	?	?	?	?	?	0	0	?	0	0	0	1	?	?	2	1	1	0	0	0	2	?	2	0	2	?	0	0	?	?	1	1	0	0	?	0	0	?	?	?	0	0	1		
Eohomalonotus sdzuyi	?	?	0	1	1	1	1	0	3	1	4	0	?	2	0	?	?	1	?	0	0	?	0	0	0	1	?	?	1	0	1	0	0	1	2	?	2	0	2	?	0	1	?	?	1	?	1	?	?	?	?	?	?	?	?	1		
Eulomina mitrata	?	?	?	1	?	0	1	0	0	1	(45)	1	?	1	0	?	?	0	0	0	0	?	1	0	1	1	?	?	1	0	0	0	0	0	2	?	2	1	?	0	?	0	?	?	1	0	1	?	?	?	?	?	?	?	?	?	?	
Flexicalymene caractaci	0	0	0	0	1	1	2	1	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	2	1	0	0	1	0	?	0	0	0	0	?	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	
Flexicalymene senana	?	?	1	0	1	1	2	1	0	1	2	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	1	0	1	0	0	0	0	?	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	
Gravicalymene capitovata	?	?	1	0	1	1	2	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	1	1	1	0	1	?	0	0	2	0	0	0	0	1	0	0	1	0	0	1	?	?	1	
Holoubkocheilus granulatus	?	?	?	0	?	1	1	0	0	1	2	1	1	2	0	0	1	0	0	0	0	1	0	0	1	2	1	1	?	0	0	0	0	0	?	?	2	1	?	?	0	0	0	?	?	1	?	?	1	?	?	?	?	?	?	?	?	0	
Homalonotus knightii	?	?	?	1	2	1	1	0	2	0	3	?	?	?	?	?	?	?	?	0	0	?	0	0	0	2	?	?	2	1	1	0	0	0	2	?	2	0	2	?	0	4	2	?	1	1	0	0	?	0	0	0	0	0	0	0	1		
Huemacaspis sp.	?	?	?	3	1	1	1	0	0	2	2	0	?	2	0	0	1	1	?	0	0	1	0	0	0	(01)	1	0	2	?	?	0	0	0	0	0	2	0	2	?	0	0	?	?	?	1	?	1	0	?	0	0	?	?	?	?	?	1	
Iberocoryphe verneuili	?	?	?	1	2	1	1	0	3	1	4	0	?	2	0	?	?	1	?	0	0	?	0	0	0	1	?	?	1	0	1	0	0	1	2	?	2	1	?	0	0	0	0	?	1	?	1	?	?	?	?	?	?	?	?	1		
Kerfornella brevicaudatus	?	?	0	3	1	1	1	0	3	0	3	?	?	?	?	?	?	?	?	0	0	?	0	0	0	0	?	?	0	1	1	0	0	1	2	?	2	0	2	?	0	0	0	?	1	?	0	2	1	0	0	?	?	?	?	?	1	
Linguocalymene linguata	?	?	0	0	1	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	2	1	2	1	?	0	1	0	1	0	0	0	2	?	0	3	2	0	0	1	0	1	0	0	0	?	?	?	?	?	1	
Liocalymene clintonii	1	1	1	3	1	1	1	0	1	1	1	0	1	2	1	0	1	0	?	0	0	1	1	0	0	0	2	0	2	1	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	1	0	?	?	?	?	?	?	0	0	1	
Liocalymene crassapensis	1	1	1	3	1	1	1	0	1	1	1	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	2	0	2	1	0	0	0	0	?	?	0	0	0	?	0	0	0	0	0	1	0	?	?	?	?	?	?	0	0	1	
Metacalymene bayliei	1	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	2	1	1	0	0	0	1	0	1	1	0	0	0	?	0	0	0	0	2	0	0	1	0	0	0	1	1	1	0	1	1	
Neseuretinus turcicus	?	?	0	0	2	1	1	0	0	2	1	0	0	1	1	0	1	0	0	0	0	1	1	0	1	2	2	0	0	0	0	0	1	0	0	0	2	1	?	1	1	1	0	?	1	0	1	0	?	0	0	?	?	?	?	?	1	
Neseuretus tristani	0	0	0	1	1	1	1	0	0	1	0	0	0	2	0	0	1	0	0	0	0	1	1	1	1	2	2	1	1	0	0	0	1	0	0	0	2	1	?	1	0	1	0	?	1	0	0	1	0	0	0	0	0	0	1	1	
Nipponocalymene hamadai	1	0	0	0	1	1	2	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	?	0	0	?	0	0	1	0	1	0	0	0	?	2	0	0	?	1	
F. Onnicalymene jemtlandica	?	?	0	0	1	1	2	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0&1	0	0	2	1	2	1	0	0	1	0	1	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0	0	1	0	1	?	0	1	
Papillicalymene papillata	?	?	?	0	0	1	1	1	0	1	1	0	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	1	?	0	0	0	2	0	1	0	1	?	0	0	?	?	?	0	1	1	
Parabathycheilus vegans	?	?	?	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	1	?	0	0	1	1	0	?	1	2	1	1	1	0	0	0	0	0	2	?	2	1	?	0	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	
Parahomalonotus forbesi	?	?	?	?	3	?	1	1	0	2	0	3	?	?	?	?	?	?	?	?	0	0	?	0	0	0	?	?	?	?	1	1	1	0	0	0	2	?	2	0	2	?	0	0	2	?	1	1	0	?	?	?	?	?	?	?	?	?	
Pharostomina oepiki	?	?	0	0	0	1	1	1	0	1	2	1	0	1	0	0	1	1	?	0	0	1	1	1	0	2	1	1	0	0	0	0	0	0	0	0	2	1	?	0	0	0	0	?	1	1	0	0	0	1	1	0	1	0	1	0	?	0	
Plaesiacomia rara	?	?	?	?	?	1	1	1	0	3	1	3	?	?	?	?	?	?	?	?	0	?	0	0	0	0	?	?	?	1	1	0	0	1	2	?	2	0	2	?	?	0	0	?	1	?	0	?	?	?	?	?	?	?	?	1		
Platycalymene duplicata	1	1	1	1	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	0	?	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	1	
Platycoryphe dyaulex	?	?	?	?	2	1	1	0	0	0	5	0	?	0	0	0	1	1	?	0	0	?	0	0	0	1	1	0	2	1	?	0	0	0	2	?	2	0	2	?	0	0	2	?	?	?	1	0	0	0	0	?	?	?	0	?	?	
Pradoella pradoi	?	?	?	0	1	1	1	0	0	1	0	1	0	2	0	0	1	0	0	0	0	1	1	0	0	2	2	0	1	0	0	0	0	0	2	?	2	1	?	0	0	1	0	?	1	0	1	0	1	0	0	?	?	?	?	?	0	
Prionocheilus pulchrum	?	?	?	0	2	0	1	0	0	1	2	1	1	2	0	0	0	0	0	0	0	1	1	0	1	2	1	0	0	0	0	0	0	0	0	1	2	1	?	0	0	0	1	?	1	0	1	1	1	1	1	0	1	1	0	0	
Protocalymene mcalisteri	?	?	0	0	1	1	1	0	0	1	5	0	0	0	0	0	1	1	?	0	0	?	1	1	0	{01}	2	1	2	1	0	0	0	0	?	?	2	1	?	0	0	0	1	?	1	0	0	1	0	0	0	?	?	?	?	?	1	
F. Reacalymene limba	0	0	0	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	0	2	1	0	0	0	1	0	0	1	0	0	1	?	0	0	1	0	0	1	?	0	0	?	?	?	0	1	1	
Reedocalymene expansa	1	0	0	0	2	0	0	1	0	1	2	0	0	0	0	0	1	1	?	0	0	1	1	1	0	3	1	0	2	0	0	1	1	0	0	0	2	1	?	0	1	2	2	?	1	?	1	0	0	0	0	?	?	?	0	0	1	
Salterocoryphe salteri	?	?	?	?	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	3	?	?	0	1	1	0	1	0	1	0	2	0	2	2	0	?	1	1	?	0	0	1	0	0	1	0	1	0	1	1	
Sarrabesia teichmuelleri	?	?	?	0	3	2	1	1	0	0	2	1	0	0	1	0	0	1	1	?	0	0	1	1	0	0	3	3	0	0	1	0	0	1	0	0	0	2	1	?	1	0	1	1	?	1	0	1	2	1	0	0	?	?	?	0	0	1	
Spathacalymene nasuta	0	0	0	1	1	1	2	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	1	?	0	3	2	1	0	1	0	?	?	0	0	?	?	?	0	0	1	
Sthenarocalymene lirella	?	?	?	?	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	1	?	0	0	0	0	1	0	1	?	?	?	?	?	0	1	1		
Tapinocalymene nodulosa	0	0	0	2	1	1	1	0	1	1	1	0	0	1	1	1	0	0	2	1	0	0	1	0	0	0	1	1	2	1	0	0	1	0	1	1	1	1	0	0	?	0	0	0	0	1	0	0	0	1	1	0	0	1	1		
Thalecalymene mammillata	?	?	0	1	1	1	1	1	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	?	0	0	2	0	2	1	0	1	0	0	1	?	?	1		
Thulincola barbarus	?	?	?	0	?	1	1	0	0	1	2	1	1	1	1	0	1	0	0	0	0	1	1	?	1	0	2	0	2	0	0	0	0	0	?	?	2	1	?	0	0	0	1	?	0	0	1	1	?	1	1	1	0	?	1	0	0	
Trimerus delphinocephalus	0	0	1	1	2	2	1	0	2	0	1	0	0	2	0	0	1	0	0	0	0	0	1	0	0	1	2	1	0	0	1	1	0	0	0	2	?	2	0	2	?	0	4	2	?	1	1	1	0	?	0	0	1	?	0	0	0	1	
Vietnamia douvillei	?	?	?	3	?	1	1	0	0	2	1	0	0	1	0	0	1	0	2	0	0	1	1	0	0	3	3	0	0	0	0	0	1	0	0	0	2	1	?	1	?	0	2	?	1	0	1	?	?	?	?	?	?	?	?	1	

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Aizanthalomina	0	1	0	0	0	?	0	1	?	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?
Acidaspis	1	0	0	1	0	0	0	1	1	1	1	0	1	1	1	1	2	?	0	1	0	1	1	1	1	0	1	1	1	1	0	1	?	?	?	?	1	1	0	?	?	0	?	1	?	0	0	0	1	2	2	1	2	0	0
Anacaenaspis	1	0	0	{01}	0	?	0	1	?	{01}	0	0	1	1	1	0	1	?	0	1	1	0	1	1	1	?	0	1	{01}	0	0	0	0	?	?	0	1	1	0	?	0	0	0	0	0	0	0	0	0	1	2	2	1	0	0	0
Apianurus	1	0	0	1	1	?	0	1	?	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	?	0	1	1	?	1	1	1	1	?	?	1	1	1	?	0	0	0	0	0	0	0	0	1	2	0	0	1
Boedaspis	1	0	0	1	0	0	0	1	?	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	1	?	?	?	1	1	?	1	1	1	1	1	?	?	1	0	1	0	2	0	0	0	0	1	0	1	2	4	2	0	0	0
Borkopleura	0	?	?	1	?	?	?	2	?	0	?	?	?	1	?	?	?	?	1	0	1	1	?	0	0	?	0	?	3	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Calipernurus	0	2	0	1	1	?	0	1	?	0	0	0	0	0	1	0	2	0	0	0	1	1	?	1	0	1	0	?	0	1	1	?	1	1	1	1	?	?	?	1	1	1	0	0	0	0	0	0	0	0	{12}	1	1	2	1	0
Ceratocara	0	?	1	1	1	?	1	1	?	0	0	0	0	{01}	1	0	0	1	0	{01}	0	0	0	0	0	0	0	?	3	?	?	?	?	?	?	?	?	?	0	1	1	?	?	?	?	?	1	1	?	?	?	?	?	?	?	1	?
Ceratocephala	0	1	1	0	0	?	1	{12}	?	0	0	0	0	{01}	0	0	{01}	1	1	{01}	0	1	0	0	0	1	0	1	1	1	0	0	0	?	1	0	1	1	1	0	1	1	4	0	1	1	1	1	1	0	1	6	?	2	1	?
Ceratocephalina	0	0	0	0	0	?	0	0	?	0	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	?	0	?	3	1	?	?	?	?	?	?	?	?	0	1	?	?	?	?	0	?	0	0	?	?	?	?	?	?	0
Ceratonurus	1	0	0	0	1	?	1	1	?	0	0	0	0	?	1	0	?	1	1	0	1	1	?	0	?	?	0	?	3	0	0	?	?	?	?	?	?	0	0	0	0	?	?	?	?	0	0	0	?	0	2	4	3	2	0	0
Chlustinia	1	0	0	?	0	?	0	0	?	1	0	0	0	0	1	0	2	?	0	0	1	1	?	0	?	?	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	0	0	?	1	2	2	2	1	0	0
Dalaspis	1	0	0	0	1	?	0	0	?	1	1	0	1	0	1	0	2	?	0	0	2	1	1	1	1	?	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	0	6	0	0	0	0	0	1	1	2	2	1	2	0	0
Diacanthaspis	0	2	0	0	1	?	0	1	1	1	0	1	1	0	1	0	1	?	0	0	0	1	1	0	0	?	0	?	1	0	1	?	0	0	0	0	0	0	2	0	1	0	3	0	0	0	0	0	1	0	1	2	{23}	2	2	0	0
Dicranurus	1	0	0	0	0	?	0	1	?	0	0	?	0	?	0	?	?	?	?	?	?	?	?	0	0	?	?	2	?	?	1	?	?	?	?	?	?	0	0	1	0	0	?	?	?	?	0	0	0	0	0	?	?	?	?	0
Dudleyaspis	1	0	0	0	1	1	0	1	?	1	0	0	0	0	1	0	2	?	0	0	1	0	2	0	1	?	0	1	1	0	0	1	?	?	?	?	1	?	?	?	?	0	0	0	1	?	0	0	0	1	2	1	1	?	0	0
Edgycombeaspis	0	1	0	1	1	1	0	0	?	1	1	0	0	0	1	0	1	?	0	0	0	1	?	?	?	?	0	?	3	0	0	?	0	?	0	0	0	?	?	0	0	0	0	1	0	?	0	1	?	{01}	2	2	0	2	1	1
Exallaspis	1	0	0	1	0	?	0	1	?	1	0	0	1	0	1	0	?	0	0	0	1	1	1	1	0	0	1	1	1	0	0	?	1	2	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	2	0	1	2	0	0
Gaotania	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	1	?	?	?
Globuliaspis	1	0	0	1	?	?	?	1	?	1	0	0	?	0	?	1	?	?	0	0	1	1	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gondwanaspis	0	3	0	1	1	?	0	1	1	1	0	0	0	0	1	1	2	?	1	0	2	1	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hispaniaspis	1	0	0	1	0	?	0	0	?	0	0	0	0	0	1	0	1	0	0	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?	1	?	?	?	?	?	?
Isoprusia	1	0	0	1	0	?	0	2	?	1	0	0	0	1	0	0	1	?	1	1	1	1	0	0	0	?	1	?	2	1	0	?	0	?	?	?	1	?	?	1	1	0	3	1	0	0	0	0	0	0	0	5	4	2	0	0
Ivanopleura	1	0	0	1	0	1	0	1	0	0	0	2	1	1	1	1	1	0	0	0	1	1	1	1	?	?	?	?	3	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	1	0
Kettneraspis	0	1	0	1	0	0	0	2	?	1	0	1	1	0	0	1	1	?	0	0	1	1	1	1	?	?	0	?	1	0	0	?	?	?	?	?	0	0	1	0	0	0	1	0	0	0	2	{012	0	2	0	0
Koneprusia	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	0	?	?	?	?	0	0	{01}	1	1	3	4	2	0	0
Laethoprusia	0	?	0	1	0	?	0	1	?	1	0	?	0	?	1	?	?	?	?	?	?	?	1	1	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	?	?	?	0	0	0	0	0	?	?	?	?	?
Leonaspis	0	1	0	1	0	?	0	0	?	1	0	0	0	0	1	0	1	?	0	0	0	1	1	1	0	0	0	?	2	0	0	?	0	0	0	0	0	0	1	1	1	0	?	1	1	0	0	0	0	2	{01}	{01}	2	2	0
Miraspis	1	0	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	?	0	1	0	1	0	?	3	1	1	?	?	?	?	?	0	0	0	0	1	5	1	0	0	0	0	0	0	2	1	4	0	0	0	0
Odontopleura	0	{01}	0	1	0	0	0	1	0	0	0	1	1	0	1	2	1	0	0	0	0	0	?	1	0	0	0	?	3	0	0	1	?	?	?	?	0	0	0	1	0	2	0	0	1	0	0	0	0	2	3	1	0	1	0
Primaspis	1	0	0	0	{01}	?	0	1	?	0	0	0	0	0	1	1	2	?	0	0	0	1	1	0	0	1	0	0	3	?	0	?	0	2	1	0	{01}	?	?	?	1	0	0	1	?	0	0	0	1	2	{23}	1	2	0	1
Procerafocephala	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	?	0	0	?	?	?	?	?	0	?	?	1	?	?	?	?	?	0	0	0	0	?	?	1	?	?	0	1	0	?	?	?	?	?	0	0	?
Radiaspis	1	0	0	?	?	?	0	1	?	0	0	0	0	0	1	0	?	0	0	0	1	1	0	?	?	0	?	0	0	0	?	?	?	?	?	?	0	?	?	?	0	2	0	1	1	0	1	0	1	2	6	4	2	0	0
Rinconaspis	?	?	0	?	?	0	0	0	?	1	0	0	0	?	1	2	0	?	1	?	0	?	?	1	?	?	1	?	?	0	0	?	?	?	?	?	?	1	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Selenopeltis	1	0	0	0	0	0	0	0	?	1	0	0	0	0	1	0	1	0	0	0	1	1	0	?	1	?	2	?	?	?	1	?	0	3	?	1	0	0	1	0	2	0	1	0	0	0	0	0	0	2	4	4	2	0	?
Selenopeltoides	1	0	0	0	1	?	0	1	?	0	0	?	2	?	?	2	?	?	?	?	?	?	0	?	?	2	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	?	?	?	?	?	0	0	0	0	?	?	?	?	?
Sinespinaspis	0	1	0	1	0	0	0	0	?	1	0	2	0	0	1	1	2	?	0	0	1	0	1	0	?	?	1	?	3	0	0	1	2	3	2	0	0	?	?	0	0	0	0	0	?	0	0	1	0	0	{012	1	0	1	0
Snoderaspis	1	0	0	0	1	?	0	1	1	1	0	0	0	0	1	1	2	?	0	1	1	0	2	0	1	?	0	1	1	0	0	1	0	?	1	?	?	1	1	0	0	2	0	1	0	0	0	0	1	2	1	1	2	0	0
Stelckaspis	1	0	0	1	0	?	0	1	?	1	0	0	0	0	1	0	1	?	0	0	2	1	1	1	1	?	1	1	?	1	0	?	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	2	0	1	2	0	0
Taemaspis	1	0	0	0	1	?	0	1	?	1	0	0	0	0	1	0	2	?	0	0	1	0	2	0	1	?	0	1	1	0	0	1	1	2	1	1	?	?	?	0	0	0	0	1	0	0	0	0	1	2	1	1	2	0	0
Uriarra	?	0	?	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	?	?	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Whittingtonia	0	0	0	0	0	?	0	1	?	0	0	0	0	1	1	1	2	1	1	0	?	?	?	1	0	1	?	1	0	0	0	0	?	?	?	?	?	1	?	1	0	0	3	0	0	1	0	1	0	1	2	6	4	0	0	0



	Acidaspis	*Anacaenaspis*	*Chlustinia*	*Dalaspis*	*Dudleyaspis*	*Snoderaspis*	*Exallaspis*	*Gaotania*	*Globulaspis*	*Primaspis*	*Stelckaspis*	*Taemasaspis*	*Unarra*	*Whittingtonia*	*Gondwanaspis*	*Apianurus*	*Boedaspis*	*Calipernurus*	*Ceratocara*	*Ceratocephala*	*Isoprusia*	*Koneprusia*
Acidaspis	0.00																					
Anacaenaspis	4.12	0.00																				
Chlustinia	4.80	4.36	0.00																			
Dalaspis	4.12	4.47	3.61	0.00																		
Dudleyaspis	4.24	4.12	3.46	3.87	0.00																	
Snoderaspis	4.47	4.24	4.12	4.47	3.46	0.00																
Exallaspis	4.24	4.00	4.36	4.36	4.47	4.47	0.00															
Gaotania	5.48	5.39	5.00	5.00	5.29	5.74	5.83	0.00														
Globulaspis	4.80	5.10	4.24	4.47	4.58	5.10	4.69	3.74	0.00													
Primaspis	5.00	4.80	4.12	4.47	4.36	4.47	4.47	5.39	4.47	0.00												
Stelckaspis	4.36	3.74	4.47	4.00	4.47	4.24	3.16	5.57	4.90	4.36	0.00											
Taemasaspis	5.00	4.36	3.74	4.12	2.83	3.00	3.87	5.66	5.00	4.00	4.12	0.00										
Unarra	5.39	5.29	5.20	5.20	5.20	5.83	5.83	2.65	4.00	5.74	5.57	5.74	0.00									
Whittingtonia	4.80	4.69	4.24	4.36	4.36	4.47	4.80	5.29	5.20	4.58	4.47	4.58	5.29	0.00								
Gondwanaspis	4.80	5.29	4.24	4.24	4.12	4.47	5.29	4.69	3.74	4.58	4.80	4.58	4.80	4.47	0.00							
Apianurus	5.57	5.39	5.00	4.90	5.00	5.00	4.58	5.66	4.90	4.36	4.80	4.47	5.74	5.20	5.10	0.00						
Boedaspis	5.20	4.90	5.10	5.29	5.29	5.29	4.00	5.83	4.90	5.00	4.24	5.00	5.66	5.20	5.20	3.74	0.00					
Calipernurus	5.57	5.39	4.47	4.69	4.90	5.10	4.47	5.74	4.69	4.24	4.80	4.36	5.66	5.10	4.69	3.00	3.87	0.00				
Ceratocara	5.48	5.39	5.00	5.29	5.00	5.29	5.39	5.20	4.69	4.80	5.57	5.20	5.39	5.00	4.58	4.47	5.29	4.58	0.00			
Ceratocephala	5.48	5.10	5.39	5.66	5.39	5.29	5.20	5.92	5.83	4.90	5.10	5.39	5.83	5.20	5.74	5.10	4.80	5.10	4.47	0.00		
Isoprusia	5.00	4.58	4.24	4.58	4.90	4.69	4.24	5.48	4.80	4.90	4.24	4.69	5.29	4.47	4.80	4.58	4.24	4.80	5.00	4.90	0.00	
Koneprusia	5.83	5.29	5.10	5.48	5.57	5.92	5.92	3.32	4.47	5.74	5.74	5.92	3.16	5.29	5.00	5.83	5.66	5.92	5.00	5.57	5.48	0.00
Laethoprusia	5.20	5.10	4.80	5.00	5.20	5.39	5.20	4.12	4.47	5.20	5.00	5.39	4.58	4.69	4.24	5.10	5.29	5.00	4.12	5.39	4.90	3.87
Acanthalomina	5.29	5.20	4.36	5.10	4.58	5.10	5.39	4.36	4.47	5.29	5.39	5.10	4.36	4.69	4.47	5.57	5.66	5.29	4.90	5.20	5.20	4.24
Borkopleura	5.57	5.48	4.69	5.20	5.00	5.66	5.57	4.12	4.12	5.10	5.74	5.48	3.74	5.00	4.69	5.57	5.66	5.20	4.90	5.48	4.90	4.47
Diacanthaspis	5.29	4.80	4.80	4.90	4.90	4.69	4.47	6.16	5.39	4.69	4.58	4.69	6.08	5.10	4.90	4.90	5.10	4.69	5.10	5.20	4.90	5.83
Edgecombeaspis	5.20	4.80	4.12	4.47	4.58	4.80	4.80	5.74	5.10	4.58	4.36	4.47	5.66	5.10	4.80	5.10	5.20	4.69	4.90	5.29	4.69	5.48
Ivanopleura	4.47	4.58	4.36	4.58	4.47	5.20	4.69	5.10	4.24	4.80	4.90	5.20	5.00	4.58	4.47	5.10	4.90	5.00	5.20	6.00	4.90	5.39
Kettneraspis	4.69	4.69	4.24	4.69	4.69	4.80	4.24	5.66	4.80	5.20	4.47	4.90	5.57	4.69	4.90	5.20	5.00	5.20	5.48	5.57	4.58	5.39
Leonaspis	5.10	4.69	4.58	4.90	5.00	5.10	3.87	6.00	5.00	4.36	3.87	4.90	6.00	5.10	5.10	4.69	4.90	4.47	4.90	4.90	4.47	6.00
Miraspis	5.20	5.29	5.10	4.90	4.80	5.20	5.29	5.74	5.00	4.80	5.20	5.20	5.74	5.10	5.29	4.12	4.47	4.58	4.58	5.20	5.20	5.66
Odontopleura	4.90	4.90	4.90	5.20	4.90	5.00	4.90	5.92	5.39	5.10	5.20	5.20	5.83	4.69	5.10	5.10	4.90	5.10	4.69	5.48	5.20	5.57
Radiaspis	5.10	4.36	3.16	4.00	3.87	4.47	4.58	5.20	4.24	4.12	4.58	4.24	5.10	4.12	4.47	4.69	4.69	4.36	4.80	5.39	4.58	5.00
Ceratocephalina	5.29	5.29	4.24	4.69	4.80	5.10	5.39	5.00	4.47	4.80	5.20	5.10	4.90	4.36	4.47	4.58	4.90	4.58	4.36	5.20	4.80	4.69
Ceratonurus	5.29	4.90	4.12	4.80	4.24	4.69	5.10	5.20	4.58	4.80	5.00	4.58	5.20	4.24	4.58	5.10	5.00	4.90	4.24	4.80	4.80	5.10
Dicranurus	5.48	5.20	4.80	5.10	5.10	5.00	5.39	4.47	4.90	5.29	4.90	5.20	4.58	4.36	4.90	5.00	5.00	5.57	4.90	5.20	4.58	4.12
Proceratocephala	5.10	5.29	4.80	5.29	5.00	5.39	5.48	5.20	4.80	5.39	5.00	5.39	4.90	4.80	4.58	5.00	4.80	4.90	4.47	5.39	5.29	5.00
Selenopeltis	5.29	4.90	4.47	4.90	4.80	5.00	4.47	5.92	5.00	4.58	4.24	4.69	5.92	5.00	5.10	4.90	4.36	4.80	5.48	5.57	4.58	5.83
Selenopeltoides	5.57	5.20	4.90	5.10	5.10	5.10	5.57	4.24	4.58	5.29	5.29	5.20	4.58	4.69	4.80	5.39	5.39	5.57	4.80	5.57	5.20	4.00
Sinespinaspis	5.10	5.00	4.36	4.90	4.47	4.69	4.80	6.00	5.29	4.69	4.58	4.24	5.83	4.69	4.90	5.39	5.39	5.10	5.48	5.74	5.00	5.83
Rinconaspis	5.39	5.00	4.24	4.80	4.80	5.10	5.29	5.10	4.90	5.39	5.29	5.00	4.90	4.80	4.69	5.57	5.29	5.39	4.80	5.48	4.58	4.47
Hispaniaspis	5.10	4.90	3.87	4.36	4.47	5.29	4.90	4.47	4.00	4.80	4.58	5.00	4.58	4.47	4.12	4.80	4.80	4.69	4.69	5.74	4.69	4.58

Laethoprusia	*Acanthalomina*	*Borkopleura*	*Diacanthaspis*	*Edgecombeaspis*	*Ivanopleura*	*Keltneraspis*	*Leonaspis*	*Miraspis*	*Odontopleura*	*Radiaspis*	*Ceratocephalina*	*Ceratonurus*	*Dicranurus*	*Proceratocephala*	*Selenopeltis*	*Selenopeltoides*	*Sinespinaspis*	*Rinconaspis*	*Hispaniaspis*
0.00																			
3.74	0.00																		
4.90	4.47	0.00																	
5.20	5.10	5.39	0.00																
5.00	4.90	5.10	4.24	0.00															
4.80	4.80	4.47	5.10	4.90	0.00														
4.80	4.47	4.80	4.47	4.24	4.12	0.00													
4.90	4.90	5.29	3.87	3.74	5.00	4.00	0.00												
5.29	5.10	5.48	4.90	5.00	4.58	4.90	5.00	0.00											
4.80	5.00	4.90	4.24	4.80	4.12	4.00	4.58	4.36	0.00										
4.80	4.47	4.36	4.69	4.58	3.74	4.36	4.69	4.58	4.24	0.00									
4.24	4.00	4.90	5.20	4.47	4.47	4.69	5.00	4.24	4.58	4.36	0.00								
4.80	4.12	4.24	4.90	4.58	4.24	4.69	5.00	4.36	4.69	3.61	4.24	0.00							
3.61	3.61	5.00	5.39	5.48	4.90	4.69	5.39	4.58	5.00	4.47	4.24	4.12	0.00						
4.47	4.12	5.10	5.20	4.69	4.47	4.69	5.00	4.00	4.12	4.47	3.61	3.87	4.24	0.00					
5.10	5.20	5.74	4.80	4.69	4.80	4.36	4.24	4.69	5.00	4.36	4.90	4.58	4.69	4.69	0.00				
3.74	3.74	4.90	5.20	5.29	5.00	5.00	5.66	4.58	4.90	4.58	4.47	3.87	2.65	4.36	4.90	0.00			
5.10	5.10	5.20	4.90	4.12	4.58	4.00	4.36	5.66	4.58	4.58	5.00	5.10	5.29	5.20	4.47	5.48	0.00		
4.24	4.47	5.00	5.57	4.80	5.00	4.90	5.29	5.48	4.90	4.47	4.58	4.80	4.69	4.90	5.20	4.80	4.69	0.00	
4.24	4.00	4.80	5.29	4.58	3.87	4.80	4.80	4.69	4.69	3.74	3.32	4.24	4.24	3.61	4.24	4.24	4.80	4.47	0.00

Appendix V: Odontopleurid taxa assigned to time slices.

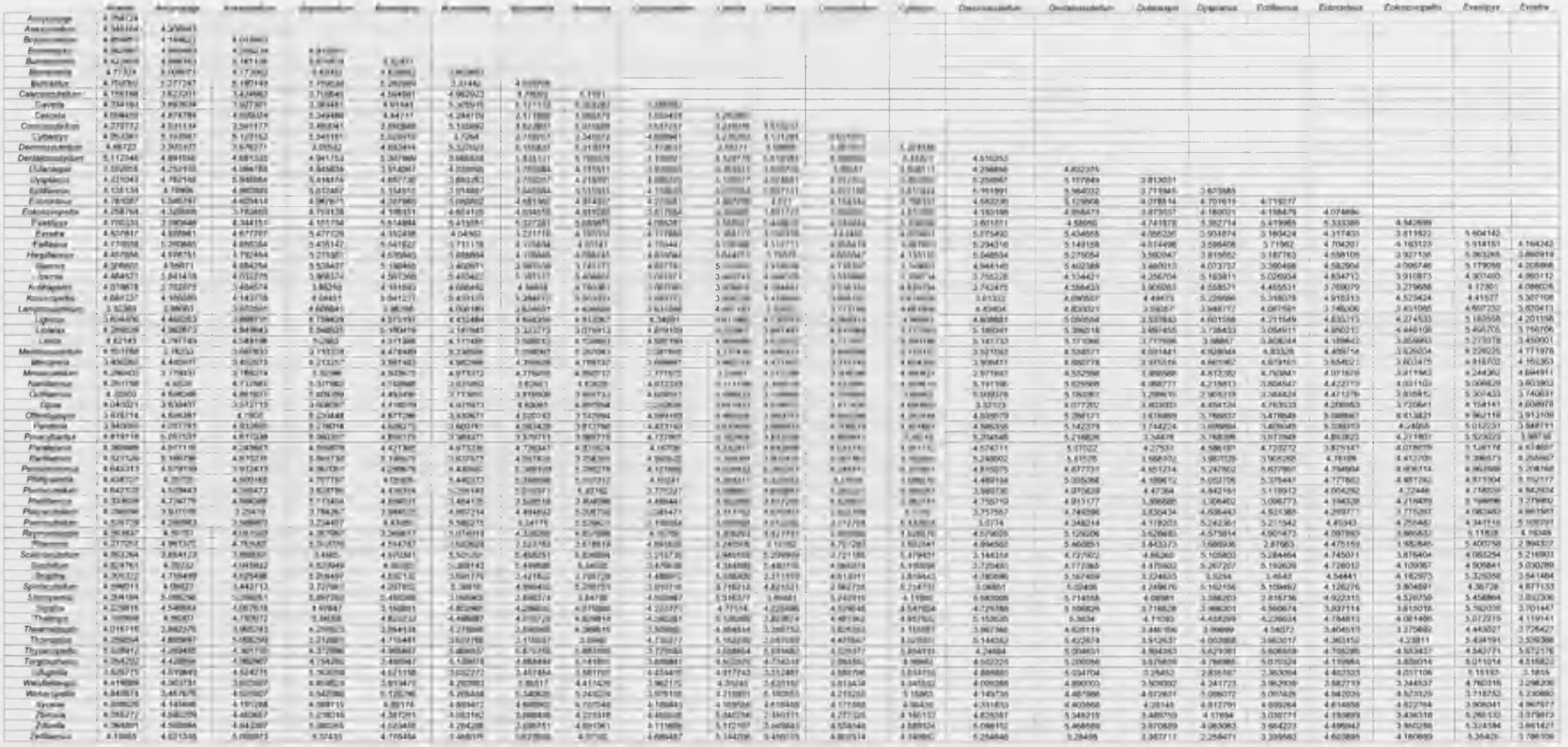
Epoch	Genus
Lower Ordovician	*Boedaspis*
	Calipernurus
	Ceratocara
	Ceratocephalina
	Chlustinia
	Selenopeltis
Upper Ordovician	*Apianurus*
	Dalaspis
	Diacanthaspis
	Hispaniaspis
	Primaspis
	Proceratocephala
	Whittingtonia
Lower Silurian	*Anacaenaspis*
	Ceratocephala
	Gaotania
	Globulaspis
	Ivanopleura
	Sinespinaspis
	Stelckaspis
Middle Silurian	*Acidaspis*
	Borkopleura
	Dudleyaspis
	Edgecombeaspis
	Exallaspis
	Laethoprusia
	Odontopleura
	Selenopeltoides
	Uriarra
Upper Silurian	*Acanthalomina*
	Leonaspis
	Miraspis
	Snoderaspis
Devonian	*Ceratonurus*
	Dicranurus
	Gondwanaspis
	Isoprusia
	Kettneraspis
	Koneprusia
	Radiaspis
	Rinconaspis
	Taemasaspis

Appendix VI: Raw sum of ranges data for all time slices for Chapter 4.

Epoch	Mean	Upper interval	Lower interval
L/M Ordovician	0	0	0
L/M Ordovician	2.479362	3.18343	1.712
L/M Ordovician	3.710796	4.21843	3.008
L/M Ordovician	4.512114	4.969	3.982
L/M Ordovician	5.130568	5.344	4.809
L/M Ordovician	5.59	5.59	5.59
Upper Ordovician	0	0	0
Upper Ordovician	2.538849	3.077	1.657
Upper Ordovician	3.833435	4.463	3.071
Upper Ordovician	4.703978	5.32104	3.891
Upper Ordovician	5.409096	5.952	4.842
Upper Ordovician	5.970167	6.308	5.581
Upper Ordovician	6.456	6.456	6.456
Lower Silurian	0	0	0
Lower Silurian	2.308954	3.108	1.62021
Lower Silurian	3.498229	4.17466	2.78821
Lower Silurian	4.293488	4.92866	3.79166
Lower Silurian	4.929194	5.45066	4.73866
Lower Silurian	5.49266	5.49266	5.49266
Middle Silurian	0	0	0
Middle Silurian	1.947644	2.85699	1.07654
Middle Silurian	2.934472	3.78699	2.001
Middle Silurian	3.581853	4.353	2.6719
Middle Silurian	4.070552	4.809	3.245
Middle Silurian	4.497286	5.116	3.843
Middle Silurian	4.815246	5.264	4.24
Middle Silurian	5.107871	5.365	4.788
Middle Silurian	5.365	5.365	5.365
Upper Silurian	0	0	0
Upper Silurian	2.241846	2.756	1.70454
Upper Silurian	3.371575	4.016743	3.096743
Upper Silurian	4.158743	4.158743	4.158743
Devonian	0	0	0
Devonian	2.086097	2.69742	1.482
Devonian	3.102601	3.704	2.543
Devonian	3.821014	4.413	3.264
Devonian	4.344387	4.875	3.785
Devonian	4.780328	5.236	4.149
Devonian	5.125106	5.562	4.59
Devonian	5.434802	5.678	5.04
Devonian	5.71	5.71	5.71

Appendix VII: Raw sum of ranges data for all clades for Chapter 4.

Clade	Mean	Upper interval	Lower interval
Acidaspidinae	0	0	0
Acidaspidinae	1.961082	2.691	0.841
Acidaspidinae	3.005455	3.789	2.084
Acidaspidinae	3.64364	4.445	2.745
Acidaspidinae	4.112867	4.86396	3.297
Acidaspidinae	4.496864	5.129	3.748
Acidaspidinae	4.785878	5.352	4.128
Acidaspidinae	5.047852	5.548	4.472
Acidaspidinae	5.27442	5.687	4.753
Acidaspidinae	5.449611	5.787	5.03
Acidaspidinae	5.62464	5.863	5.287
Acidaspidinae	5.769347	5.896	5.47
Acidaspidinae	5.896	5.896	5.896
Apianurinae	0	0	0
Apianurinae	2.167143	2.437	1.982
Apianurinae	3.24	3.24	3.24
Ceratocephalinae	0	0	0
Ceratocephalinae	2.027112	2.65366	1.31036
Ceratocephalinae	3.056609	3.42866	2.34336
Ceratocephalinae	3.670196	3.80648	3.27848
Ceratocephalinae	4.08348	4.08348	4.08348
Odontopleurinae	0	0	0
Odontopleurinae	2.260056	2.91258	1.47446
Odontopleurinae	3.362607	4.05801	2.663
Odontopleurinae	4.113462	4.88655	3.33254
Odontopleurinae	4.67848	5.396	3.983
Odontopleurinae	5.146421	5.817	4.5
Odontopleurinae	5.495958	6.11455	4.866
Odontopleurinae	5.82501	6.387	5.185
Odontopleurinae	6.138615	6.597	5.496
Odontopleurinae	6.367396	6.767	5.754
Odontopleurinae	6.615367	6.896	6.015
Odontopleurinae	6.813732	7.013	6.236
Odontopleurinae	7.013	7.013	7.013
Selenopeltinae	0	0	0
Selenopeltinae	1.958728	2.241257	1.034
Selenopeltinae	2.913608	3.265907	2.551
Selenopeltinae	3.59	3.59	3.59



Appendix VII- Interbeam Euclidean distance analysis values for Chapter 5. Values are in units of character state differences.

Fadfaena	Hegidiarmus	Ifiarnus	Izarnia	Kudhapelfix	Kosmogaelfin	Langmoorfelfish	Lajlesia	Limelax	Lolax	Mentiloscaldfish	Merogaris	Metascaldfish	Mesdiferox	Orfilfaenia	Ojosa	Otterdyespix	Panderia	Paradykardyx	Parakjurus	Parifaenus	Petrochoclonus	Philipsinella	Planiscaldfish
3.94068																							
4.077863	3.89963																						
5.00033	4.790629	5.007162																					
4.423333	4.63747	4.479639	3.913948																				
5.529848	4.821781	5.448731	5.983732	3.817423																			
4.373162	4.187525	4.166893	4.449929	3.366849	4.633961																		
4.556398	4.139676	4.369868	4.537419	4.07704	4.605057	3.546893																	
3.911371	3.627899	3.349168	5.148523	4.13833	5.257919	4.941572	4.217958																
3.809000	3.645686	4.097307	5.104719	4.171453	5.178539	3.718971	4.867153	3.783884															
4.809560	4.122155	4.809504	2.161721	3.236388	3.990744	4.272931	4.934153	5.012694	4.868086														
4.712711	4.474851	4.624586	5.082088	3.182184	4.196639	3.390369	4.1586	4.880701	4.41215	3.939437													
4.841778	4.64883	4.628081	3.254587	3.066970	3.664963	4.106182	4.835376	4.807282	4.840353	2.931162	3.1885												
4.515124	4.024097	3.882813	4.872666	4.099412	5.161106	3.643546	5.014866	4.543789	3.7788	4.834432	4.281219	4.158731											
3.611628	3.142112	3.368434	4.957256	4.486415	5.089521	3.891551	4.491086	3.486828	3.74744	4.19689	4.218156	4.637424	4.378984										
4.544653	4.121455	4.169417	5.082824	3.932699	4.729444	3.899097	4.706219	4.089604	4.462263	2.738838	3.218137	3.409588	4.636623	4.466817									
4.24967	4.013438	3.50174	3.98756	4.316373	5.006304	3.796482	4.069868	3.622897	4.27298	4.349296	4.69967	4.623577	4.09485	3.348986	4.434739								
4.069312	3.824088	3.574397	4.918854	4.286321	5.054978	3.846231	4.144672	3.891237	4.094175	4.842137	4.712861	4.725268	4.301894	3.911154	4.490741	3.22456							
3.32614	3.764348	3.609643	5.11078	4.756347	5.492649	4.176284	4.9391	3.991886	3.782675	4.82 1258	4.531338	4.801467	4.143466	3.536334	4.597555	3.873954	3.937839						
4.549646	4.384962	4.857965	4.104405	3.526955	4.660708	4.276273	4.364918	4.007787	4.211596	3.880873	4.498487	4.879557	4.251761	4.168484	4.054717	4.854517	4.69753	4.620611					
4.000639	3.981989	3.984654	5.056658	4.983774	5.953093	4.324758	4.948731	3.48536	3.82323	5.189887	4.95799	5.022844	4.487234	3.956504	4.842501	3.908031	3.87114	5.111651	5.049128				
5.15851	5.38024	5.490484	4.961997	4.343455	5.178308	5.089076	4.814529	4.980921	5.123487	4.737193	4.139862	4.389625	5.101467	5.317533	4.251598	5.04371	5.190237	5.119339	5.0454	5.419435			
5.179845	5.059658	5.183635	4.288152	4.109454	4.886042	4.376735	4.508763	5.356524	5.053043	3.94503	3.887228	4.121392	5.196447	5.094376	5.704943	5.093502	5.142335	4.959216	4.587551	5.338263	4.361249		
4.693014	4.615247	5.151643	4.318977	3.72475	3.959851	4.224477	4.747951	5.270246	4.826244	3.909588	3.973589	3.834607	4.01306	4.636578	3.765363	5.034887	5.084284	5.11313	4.020685	5.139058	5.08176	4.447041	
3.116427	3.72438	3.363441	5.148746	4.914238	5.114409	3.095851	3.847951	5.109059	3.7506668	4.915987	3.972311	4.284043	4.230953	3.226384	3.667659	3.38094	3.46386	3.146206	4.149581	5.024863	5.00082	4.818188	4.858145
4.795896	4.61625	4.809622	3.834421	3.219506	4.199211	3.614347	4.427538	4.994485	4.411747	5.489034	4.91038	5.28784	4.297891	4.873179	3.521101	4.711269	4.764042	4.689068	3.860557	5.015885	3.898674	4.129237	4.168162
5.010381	4.884629	5.200291	3.835806	3.514507	4.178779	4.347895	4.527831	5.244277	4.95725	3.999396	3.967078	3.810754	5.102118	5.088942	3.100282	5.035567	4.884403	5.194295	4.000777	5.428328	4.603802	4.48656	4.024259
4.596689	4.488679	4.698461	4.804729	3.882704	4.586228	3.835419	4.564316	4.796658	3.998883	4.508349	3.778514	4.102151	4.311561	4.10809	3.78861	4.704685	4.757511	4.441221	4.049598	4.604997	4.178226	3.798525	4.287569
3.659113	3.432613	3.318266	4.867529	4.483157	5.234184	4.068892	4.382189	5.210342	3.842231	4.749058	4.643199	4.519862	3.87119	3.943113	4.484175	3.358205	3.28294	3.982163	4.615089	3.408576	5.479268	5.14475	4.636519
4.915389	4.890102	5.108763	3.285849	3.883402	3.701349	4.696465	4.826111	5.507987	4.853617	3.068211	4.052511	3.555344	5.171457	4.987967	3.507775	5.266182	5.121828	5.309123	4.139121	5.378704	5.023965	4.692781	3.605439
5.048611	4.887866	5.093276	3.346851	4.063426	3.88844	4.490434	4.706018	5.33101	4.879092	3.552898	4.39137	3.838277	5.2566-1	5.191268	3.793468	5.197118	5.050791	4.963528	4.467101	5.391481	4.875251	4.216092	4.081926
3.527159	3.734714	3.471163	4.754415	4.36886	5.234408	3.850388	4.141186	5.492182	3.963022	4.631875	4.33071	4.498529	4.286114	3.996736	4.299589	3.456652	3.528213	3.30802	4.695087	3.800242	5.082474	4.931876	4.701311
5.079422	4.80044	5.13113	3.934733	3.373693	3.885228	4.173199	4.573818	5.185352	4.878423	3.649432	3.973396	3.788217	4.994219	5.014949	3.480437	5.144119	5.192476	5.15926	3.851236	5.477129	4.496537	4.368511	4.277566
4.113073	3.803878	3.378478	5.320605	4.747425	5.531678	4.225518	4.883942	5.444689	4.342643	5.003249	5.021944	5.084119	3.511558	3.737758	4.952362	3.567787	3.497035	3.915848	4.842212	4.011663	5.757155	5.33755	5.104706
4.307349	4.296077	4.345279	3.853136	3.753241	4.771475	3.902384	4.477342	4.844881	3.491728	4.343994	3.582634	3.407725	3.853214	4.278147	3.903084	4.480573	4.424442	4.282967	4.496136	4.621266	4.344352	4.08907	4.505843
4.868921	4.927988	4.32543	4.758086	4.086078	5.081701	5.484168	4.983134	4.881633	4.58468	4.150198	4.267384	4.638514	3.655983	4.399801	4.448646	4.01739	3.826209	4.771967	4.639472	4.95156	5.076654	5.122311	5.183795
4.138167	3.971908	4.223882	4.209901	3.30875	4.286014	2.99328	4.274802	4.826368	3.947258	3.981652	3.487462	3.821104	4.563949	3.818738	3.522728	4.137636	3.964902	4.146089	3.778206	4.289661	4.310463	4.333743	4.193988
4.238486	4.068213	3.774533	5.089384	4.323816	5.323541	3.848904	4.774803	5.012486	4.178801	5.003645	4.643426	4.738815	5.071421	5.08756	4.732566	4.215807	4.156102	3.964215	4.622996	4.114199	5.223656	5.104109	5.058589
5.414628	5.061982	5.500982	3.970857	3.729001	3.910752	4.957992	5.038376	5.308796	5.213644	3.884882	4.426767	3.148146	5.41581	5.503824	4.002906	5.767149	5.535642	5.860369	4.276199	5.796036	4.733929	4.68597	4.180266
4.693554	4.576414	4.806747	4.144329	3.814791	4.691207	3.819842	4.9024	5.111598	4.248984	3.791089	3.944143	4.308811	4.618857	4.812723	3.919491	4.785831	4.733021	4.886531	4.053232	5.047282	4.116331	3.706852	4.338625
3.418678	2.737046	3.468011	4.842573	4.330818	4.845473	3.482454	3.927085	5.019869	3.489749	4.882677	4.348182	4.094438	3.94801	3.965274	4.361044	3.249194	3.171342	3.106925	4.333952	3.442183	4.980949	4.896353	4.664754
4.055556	4.536856	4.182464	4.141276	3.217263	4.674838	3.315545	3.964255	4.708958	3.628183	3.961372	3.298838	3.844235	4.168875	3.786881	3.742114	4.054938	4.116112	4.048901	3.815724	4.319983	4.226358	4.343697	4.342356
5.354126	4.976204	4.861858	4.021345	4.166642	4.676196	4.584805	5.161061	5.213958	5.101724	4.196514	4.775388	4.274105	4.778143	5.046562	4.256694	4.901988	4.746572	5.545386	5.096582	5.290562	5.090613	4.757154	4.659629
4.728312	4.692536	4.837928	4.635159	4.16652	4.7958	4.3604	4.380486	4.712217	4.709585	4.498208	4.375473	4.164836	5.083801	4.838563	4.560451	4.614929	4.800363	4.264546	4.89553	4.880664	4.799192	4.639175	
4.031154	3.826448	3.893333	4.726103	4.234592	4.671522	3.19829	4.486471	5.585064	3.509881	4.628853	4.167152	4.487412	3.328581	3.428105	4.396357	4.051789	3.989629	3.681319	4.642552	4.187076	5.174404	5.00851	4.719277
4.142869	3.956656	4.446723	4.944787	4.284239	5.098947	3.363411	4.859664	4.152968	3.553158	4.648875	4.471573	4.819605	3.94382	3.888421	4.536301	4.420073	4.363164	3.922506	4.643736	4.392263	5.068732	4.64019	4.824134
3.842079	3.743237	4.721239	5.041009	4.661568	5.084284	3.823556	4.442184	5.427729	3.913457	4.921594	4.807284	4.809578	3.681122	3.538096	4.592078	3.398531	3.323667	3.618811	4.612811	3.815803	5.339699	5.101435	4.825486

Appendix VIII: Intertaxon Euclidean distance analysis values for Chapter 5. Values are in units of character state differences.

Platilaenus	*Platyscutellum*	*Poroscutellum*	*Raymondaspis*	*Rhaxeros*	*Scelvitrocutellum*	*Scutellum*	*Snaptria*	*Spinoscutellum*	*Stenoparesia*	*Stygina*	*Thalesys*	*Theametaspis*	*Thometlus*	*Thysanopeltis*	*Turgicephalus*	*Ulugtella*	*Waisfieldaspis*	*Weberopeltis*	*Xyoeax*	*Zbirovia*	*Zdicella*
4.511037																					
4.767933	3.837767																				
4.09966	3.379683	4.35763																			
3.909796	4.340633	5.08418	4.369134																		
5.022547	3.803489	3.481779	4.822472	5.11188																	
4.799343	4.086256	3.741627	4.313366	5.054981	3.82402																
2.913423	4.511823	4.900408	4.099308	2.73312	5.010002	4.964343															
4.723088	2.630211	3.445543	3.857448	5.106864	3.820075	3.846022	4.921126														
3.829138	5.066887	5.679173	5.11048	3.318023	5.595811	5.509141	3.544912	5.531614													
4.018168	3.88009	4.533739	3.128529	4.066037	4.709644	4.321546	4.120706	4.21893	4.585782												
4.644699	4.324697	4.957104	4.528427	4.260685	5.165142	5.090126	4.252987	4.836175	4.135189	4.174738											
3.778589	3.390749	3.982864	3.539643	4.022718	4.218551	4.362264	3.933291	3.639883	4.266706	3.485503	3.584342										
3.801077	4.443682	5.190141	4.35718	3.723407	5.325747	5.369124	3.664409	4.870532	3.879987	4.337324	3.962077	3.503636									
5.328229	4.117727	3.823079	4.875717	5.673462	5.192761	4.197503	5.536916	4.138604	5.870927	5.025815	5.496055	4.501159	5.679912								
4.560731	3.454164	4.47174	2.924921	4.829276	4.346302	4.149034	4.496899	3.907964	3.046833	3.148568	4.207416	3.321441	4.642447	4.671783							
3.018335	4.414342	4.864417	4.381336	2.9436	4.90876	4.807944	2.811763	4.840618	2.774275	3.941999	3.853228	3.651590	3.23501	5.351593	4.557736						
3.434616	3.245346	4.006027	3.275211	3.927033	4.474439	4.389121	3.600463	3.528709	4.485488	3.475668	4.359754	3.172044	3.763562	4.815552	3.751686	3.70977					
5.111194	4.519738	4.42108	4.786468	5.19581	4.194054	4.517841	5.309161	4.567414	5.383878	4.967866	4.822434	4.207901	5.200354	4.650147	4.824834	4.958576	4.931795				
4.343564	4.093994	4.115287	4.757679	4.816686	4.845622	4.997965	4.554995	4.215009	4.820588	4.680287	5.023383	4.124782	4.815734	4.902243	4.887433	4.393247	4.230389	4.210949			
3.777167	4.333258	4.845973	4.25958	3.204528	4.936551	4.964877	3.41076	4.539799	3.868213	4.009962	3.730073	3.181885	3.774351	5.462324	4.381341	3.132768	3.5754	4.937118	4.727642		
4.275123	4.367429	5.04086	4.309848	3.754479	5.029588	5.293721	3.682405	4.717486	3.967347	3.933303	3.732404	3.325589	2.969459	5.579784	4.160796	3.145093	3.883323	5.261144	4.902967	2.221263	
3.626069	4.629781	5.141305	4.58943	3.31221	5.198008	5.327328	3.044331	5.081009	2.79855	4.106497	3.851015	3.893151	3.656837	5.663635	4.760436	2.250671	4.005128	5.187111	4.727541	3.779727	3.598783

Appendix IX: Illaenoidea taxa assigned to time slices.

Epoch	Genus
Lower Ordovician	*Dysplanus*
	Ottenbyaspis
	Panderia
Middle Ordovician	*Dulanaspis*
	Ectillaenus
	Harpillaenus
	Illaenus
	Nanillaenus
	Perischoclonus
	Platillaenus
	Theamataspis
	Turgicephalus
	Waisfieldaspis
	Zbirovia
Upper Ordovician	*Alceste*
	Bronteopsis
	Bumastoides
	Cekovia
	Eobronteus
	Eokosovopeltis
	Failleana
	Lamproscutellum
	Octillaenus
	Parillaenus
	Phillipsinella
	Snajdria
	Stenopareia
	Stygina
	Thaleops
	Ulugtella
	Zdicella
	Zetillaenus
Lower Silurian	*Bumastus (Bumastella)*
	Bumastus (Bumastus)
	Cybantyx
	Ligiscus
	Litotix
	Meroperix
	Opoa
	Planiscutellum
	Rhaxeros
	Thomastus
Upper Silurian	*Avascutellum*
	Decoroscutellum
	Excetra
	Kosovopeltis
	Liolalax
	Paracybantyx
Lower Devonian	*Bojoscutellum*
	Comuscutellum
	Dentaloscutellum
	Izarnia
	Kolihapeltis
	Meridioscutellum
	Metascutellum
	Paralejurus
	Platyscutellum
	Poroscutellum
	Spiniscutellum
	Xyoeax
	Weberopeltis
Middle Devonian	*Exastipyx*
	Raymondaspis
	Ancyropyge
	Calycoscutellum
	Cavetia
	Scabriscutellum
	Scutellum
	Thysanopeltis

Appendix X: Raw sum of ranges data for all time slices for Chapter 5.

Epoch	Mean	Upper interval	Lower interval
L Ord	0	0	0
L Ord	12.070877	16.10754	3.632206
L Ord	17.844079	17.844079	17.844079
M Ord	0	0	0
M Ord	16.20241	20.551694	12.173475
M Ord	24.230263	28.282906	20.382012
M Ord	29.33791	32.866683	25.483118
M Ord	33.114896	36.428471	29.368334
M Ord	36.171009	39.117422	32.793018
M Ord	38.542531	41.277486	35.314513
M Ord	40.747579	42.93453	37.548245
M Ord	42.55375	44.32003	40.380653
M Ord	44.080908	45.350489	41.903941
M Ord	45.502876	45.502876	45.502876
U Ord	0	0	0
U Ord	16.878856	21.279008	11.353004
U Ord	25.396611	29.83691	20.663456
U Ord	30.767432	35.214634	25.66065
U Ord	34.599269	39.243665	29.657719
U Ord	37.534848	41.604754	33.016213
U Ord	40.157175	44.167088	35.992706
U Ord	42.328748	46.06203	38.275373
U Ord	43.889468	47.320138	40.269249
U Ord	45.469191	48.58466	41.780935
U Ord	46.823068	49.710759	43.421431
U Ord	48.032295	50.677498	45.085597
U Ord	49.135532	51.556402	46.298478
U Ord	50.29708	52.279043	47.589637
U Ord	51.210424	52.858536	48.962466
U Ord	52.066533	53.273099	50.264247
U Ord	52.844267	53.600499	50.991596
U Ord	53.600499	53.600499	53.600499
L Sil	0	0	0
L Sil	16.876415	20.866356	12.982971
L Sil	25.178195	28.469515	21.212834
L Sil	30.688305	33.79851	26.927201
L Sil	34.435827	37.478447	31.208556
L Sil	37.440695	40.104932	34.492241
L Sil	40.019984	42.170079	36.918383
L Sil	41.990975	43.622906	39.812106
L Sil	43.877571	44.84987	41.905431
L Sil	45.450265	45.450265	45.450265
U Sil	0	0	0
U Sil	16.831298	20.076355	13.982723
U Sil	25.224198	27.982126	22.598008
U Sil	30.373663	32.134647	28.930181
U Sil	33.946836	34.911298	33.216564
U Sil	36.756279	36.756279	36.756279
L Dev	0	0	0
L Dev	15.747479	20.14829	10.946766
L Dev	23.880792	28.455944	18.709998
L Dev	29.116893	33.528226	23.214348
L Dev	32.890668	36.882557	27.226912
L Dev	36.009752	39.854753	31.217586
L Dev	38.465055	41.808384	33.662665
L Dev	40.486711	43.62003	36.781192
L Dev	42.34021	44.992112	38.77754
L Dev	43.853777	46.0445	41.012128
L Dev	45.329266	47.040851	42.930173
L Dev	46.631501	47.51696	45.31988
L Dev	47.797264	47.797264	47.797264
U Dev	0	0	0
U Dev	16.264969	20.91483	12.550446
U Dev	24.580946	28.589973	20.761665
U Dev	29.943356	32.96424	26.400065
U Dev	33.755624	36.474315	30.356659
U Dev	37.120335	39.310229	35.235037
U Dev	39.738554	41.222432	38.245697
U Dev	42.001251	42.001251	42.001251

Appendix XI: Raw sum of ranges data for all clades for Chapter 5.

Clade	Mean	Upper interval	Lower interval
Clade A	0	0	0
Clade A	14.446099	19.819685	10.225522
Clade A	21.809574	26.621055	17.094237
Clade A	26.323328	30.992373	21.307894
Clade A	29.92982	33.973265	24.992919
Clade A	32.508386	35.954708	27.645265
Clade A	34.908356	38.031382	29.97265
Clade A	36.619345	39.279237	31.904674
Clade A	38.272797	40.446753	34.389951
Clade A	39.661125	41.51599	37.899942
Clade A	40.801564	42.429714	39.42745
Clade A	41.806091	42.69736	40.727653
Clade A	42.69736	42.69736	42.69736
Clade B	0	0	0
Clade B	14.556055	17.977804	10.740593
Clade B	22.139634	25.827756	19.6562
Clade B	26.699032	29.360109	24.270479
Clade B	29.965474	32.321497	28.419002
Clade B	32.254507	33.315287	31.04127
Clade B	33.978425	33.978425	33.978425
Clade C	0	0	0
Clade C	13.744594	15.904201	11.37738
Clade C	20.614547	22.017283	19.193246
Clade C	25.095408	25.095408	25.095408
Clade D	0	0	0
Clade D	14.188674	17.705095	3.632206
Clade D	21.35243	25.158896	17.550388
Clade D	25.60095	27.86059	20.894125
Clade D	28.384566	29.476523	27.134723
Clade D	30.26935	30.26935	30.26935
Clade E	0	0	0
Clade E	17.131804	20.562325	13.314448
Clade E	25.602363	28.749003	21.254825
Clade E	31.311328	34.515256	27.605857
Clade E	35.487105	38.699897	32.168095
Clade E	38.999376	41.128745	36.130917
Clade E	41.735747	43.607796	39.947793
Clade E	43.992356	45.310753	43.063703
Clade E	46.027916	46.027916	46.027916
Clade F	0	0	0
Clade F	12.924791	16.073727	7.267011
Clade F	19.525693	21.983034	16.279681
Clade F	23.765518	26.313072	21.443533
Clade F	26.905087	28.518066	25.037789
Clade F	29.37903	29.37903	29.37903